The ecology of vascular epiphytes on a *Ficus* L. host (Moraceae) in a Peruvian cloud forest

by

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Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution, and to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

Signed

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Abstract

A total of 190 holoepiphytic and 5 hemiepiphytic vascular plant species were collected from the canopy and the trunk of an emergent *Ficus* L. species host that is common to a Peruvian cloud forest. One hundred and fourteen of the vascular epiphyte species were orchids. A large majority of the vascular species were rare in occurrence. Vascular epiphyte diversity and density was highest in the outer canopy zone of the host crown. In the inner canopy zone there was a dearth of epiphytes, attributed to a high rate of epiphyte slumping on the smooth-barked branches. The trunk had a different suit of species to those found in the canopy.

During the wet season, the thickening of epiphytic matter in the outer canopy zone appeared to contribute to a large amelioration of daytime and nocturnal temperatures through evaporation and heat retention respectively. Nocturnal temperatures were highest in the outer canopy zone, and were lowest on the forest floor. The latter was attributed to the downward flow of the product of radiative cooling as a result of the heterogeneous canopy on the steep slope.

Epiphyte clumps appear to slump before competition causes the loss of early successional species. Some species showed a preference for more shaded epiphyte clumps and many were more frequent on smaller branch diameters. Most species showed a moderately high niche overlap with a large number of other species, which suggested a high degree of species coexistence.

Epiphyte slumping is suggested to be the major driving mechanism for the maintenance of non-equilibrium in the community. Aspects of the phenologies of epiphytes, age-structure of the community and high environmental variation could be other mechanisms for the maintenance of a high degree of species coexistence.

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Chapter 1 Introduction

1.1 Background

Vascular epiphytes account for c.10% of global vascular plant diversity (Kress, 1986). The epicentre for vascular epiphyte diversity is the neotropics (Benzing, 1990; Madison, 1977), which is also home to the largest proportion of the worlds plant species (Gentry, 1982b; Henderson *et al.*, 1991; Myers *et al.*, 2000; Phillips *et al.*, 1994). The vast majority of neotropical vascular epiphyte species are concentrated in montane forests (Gentry and Dodson, 1987b), where the epiphyte component can represent up to 30% (Gentry and Dodson, 1987a) or 50% (Bussmann, 2001; Kelly *et al.*, 1994) of the total vascular plant flora. The peak in vascular epiphyte diversity within the neotropics occurs at mid elevations of 1500 – 2500 m asl (Freiberg and Freiberg, 2000; Hietz and Hietz-Seifert, 1995a; Vazquez and Givnish, 1998; Wolf, 1994; Wolf and Alejandro, 2003). These patterns of epiphyte diversity are explained by the higher alpha diversity, and higher species turnover between sites, in montane forest relative to lowland forest (Nieder *et al.*, 1999).

Tropical montane forests are characterised by a cool and humid atmosphere. This appears to contribute to the growth of epiphytic plants in the canopy at high densities (Figure 1). Epiphyte communities play an influential role in montane forest ecosystem processes by contributing stripped cloud water and nutrients that would otherwise remain unavailable to the forest (Clark *et al.*, 1998a; Clark *et al.*, 1998b; Coxson, 1991; Coxson *et al.*, 1992; Coxson and Nadkarni, 1995; Nadkarni, 1986). Epiphyte communities are important habitat for insects (Floater, 1995) and amphibians (Giaretta *et al.*, 1999; Pounds, 2000; Pounds *et al.*, 1999), and are food source for birds (Nadkarni and Matelson, 1989) and canopy mammals (pers. obs.). Epiphyte communities can also directly benefit host trees, as evidenced in some tropical species by the evolution of adventitious canopy roots to harness the nutrient pool held by epiphyte communities upon their upper branches (Nadkarni, 1981, 1994).

Figure 1: A large epiphyte clump containing 13 vascular species on a branch (12 cm diameter) 24 m above the forest floor in a Peruvian montane cloud forest.

The floristic composition of moist species rich epiphyte environments are commonly characterised by species rich genera of a few families (Bøgh, 1992; Bussmann, 2001; Ingram *et al.*, 1996). Families that commonly contribute the majority of species in neotropical montane epiphyte floras are the Araceae, Bromeliaceae, Ericaceae, Orchidaceae, Piperaceae and a number of fern families amongst others. Endemism in montane epiphyte floras is high, particularly within the tropical montane cloud forests, where local endemism may reach 25% due to the rapid speciation in relative isolation within some genera (Gentry, 1982a, 1986). By far the greatest proportion of epiphyte diversity is attributed to the Orchidaceae (Kress, 1986; Madison, 1977). Orchids commonly represent the largest number of epiphyte species in primary forests throughout the tropics (Bussmann, 2001; Catling and Lefkovitch, 1989; Dagar and Jeyamurthy, 1990; Freiberg, 1999; Hietz and Hietz-Seifert, 1995a; Johansson, 1974; Nieder *et al.*, 2000; Nkongmeneck *et al.*, 2002; ter Steege and Cornelissen, 1989; Zimmerman and Olmsted, 1992).

Single host trees can accumulate a high diversity of vascular epiphyte species. Previously reported figures include 107 spp. (Valdivia, 1977) and 109 spp. (Nowicki, 1998). Despite the frequent recording of diverse and apparently coexistent populations within epiphyte communities, there have been few attempts to determine the mechanisms that influence the arrangement of species (Bennett, 1986; Benzing, 1981; Hietz, 1997; Zotz, 1995). There are no such accounts known to the author that were derived from a vascular epiphyte community of high diversity.

Preferences of vertical distribution by epiphyte species influence the spatial arrangement within host trees and forests of both non-vascular (Cornelissen and ter Steege, 1989; Pentecost, 1998) and vascular epiphytes (Bøgh, 1992; Freiberg, 1996; Hietz and Hietz-Seifert, 1995b; Ingram and Nadkarni, 1993; Johansson, 1978; Pupulin *et al.*, 1995; Rudolph *et al.*, 1998; ter Steege and Cornelissen, 1989). Though many studies have now addressed the three-dimensional aspects of epiphyte distribution, the vast majority were undertaken in lowland forest canopies. Microclimatic differences between lowland and montane canopies are likely to influence the distribution of epiphytes. This may explain the differences in diversity, density and ecosystem roles observed between lowland and montane epiphyte communities, though data has not been forthcoming.

An association between the spatial distribution of epiphyte species and variation in solar radiation is commonly accepted. This has been deduced from observations and laboratory experiments (Griffiths and Smith, 1983; Griffiths *et al.*, 1984; Haslam *et al.*, 2003; Stancato *et al.*, 2002). Though there is no doubting the differences in photosynthetic efficiencies of different species, to date there has been no work known to the author that determines the variation of radiation receipt and extinction within tree crowns. Furthermore, and as pointed out by Zotz and Hietz (2001), much work has been concentrated on a few species from the outer edge of the canopy, leading to misleading concepts of the physiological tolerances of a typical epiphyte.

The Orchidaceae is particularly well adapted to epiphytic life. Commonly displayed traits include morphological and physiological adaptations to cope with transient water and nutrient supply (Benzing, 1990; Benzing *et al.*, 1983; Oliveira and Sajo, 1999), the production of millions of tiny dusts seeds for carriage to higher branches (Benzing, 1987; Madison, 1979), mycotrophy for seed nutrition at germination (Yoder *et al.*, 2000), and specialized pollinator relationships (Benzing and Atwood, 1984). Many of the other epiphyte specialists such as the Araceae and Bromeliaceae, have their own peculiar set of adaptations to subsist in the canopy (Benzing and Davidson, 1979; Benzing and Renfrow, 1974; Mantovani, 1999). Hemiepiphytes, which only spent a part of their lifecycle in the canopy, also share common physiological and morphological traits with true epiphytes (Patiño *et al.*, 1999; Williams-Linera and Lawton, 1995). By far the largest range of vascular epiphyte lifeforms can be found in montane cloud forest (Benzing, 1987), and even there, where moisture regimes are optimal, many epiphytes can be found with xeric adaptations (Hietz and Briones, 1998).

However, our current understanding of the physiology of epiphytes is highly biased by a few well-studied taxa from a small number of ecosystems (Zotz and Hietz, 2001). Few montane species have been investigated. In fact, many montane species are likely to be undiscovered due to a dearth of collections (Gentry and Dodson, 1987b). This has been a barrier to taxonomic work in montane genera, that in turn, acts as a deterrent to undertaking local and regional epiphyte floras, of which there are few. The dearth of knowledge on montane epiphytes is epitomized in Peru, where collections and catalogues (Brako and Zarucchi, 1993) are completely inadequate (Gentry, 1992; León and Young, 1996), even relative to adjoining countries.

Studies on the dynamic processes in any epiphyte community are few (Ackerman *et al.*, 1996; Bennett, 1986; Larson, 1992; Zotz, 1995; Zotz and Vollrath, 2002) compared to the number from of other plant communities. Such studies in epiphyte communities from montane ecosystems are rare (Hietz, 1997; Hietz *et al.*, 2002). The lack of studies from all environments is in partly a result of the difficulties in making time-series observations from the canopies of trees. Our dearth of knowledge of epiphyte population dynamics

from montane environments relative to lowland ones is ironic, given that it is therein they have by far the greatest influence on ecosystem processes.

The following study presents the results of an investigation of many ecological aspects of a Peruvian cloud forest epiphyte community. The present study was undertaken with a holistic approach, given the dearth of knowledge of epiphyte ecology in this environment. A wide range of ecological themes were concurrently addressed from within and around a single emergent *Ficus* host.

1.2 Research Aims

The aims of the research were to determine within a single *Ficus* host tree in a montane cloud forest:

1. the structure and flora of the epiphyte community
2. the distribution of the epiphyte flora in relation to habitat characteristics
3. the microclimatic profile of the canopy;
4. the dynamics of the epiphyte community;
5. the mechanisms influencing species distribution and associations in the upper canopy.

In conclusion, the collective results will be presented in order to describe a dynamic ecological model that suggests an explanation for the creation and maintenance of the patterns of epiphyte diversity and distribution observed from the *Ficus* host.

1.3 Structure of thesis

The second chapter presents the details of the study area and the methodology used in data collection and production.

The third chapter investigates the structure and composition of the epiphyte community in order to address the first research aim.

The forth chapter investigates the habitat characteristics and distribution of the epiphyte community in order to address the second research aim.

The fifth chapter investigates the microclimate of the forest canopy in order to address the third research aim.

The sixth chapter investigates the community dynamics of the epiphyte community in order to address the forth research aim.

The seventh chapter investigates the species distribution and associations of the upper canopy epiphyte community in order to address the fifth research aim.

The last chapter collates the relevant findings to describe the dynamic ecological model and summarises all research chapters in the conclusion.

Chapter 2 Methods

2.1 Study Area

This study was conducted in lower tropical montane cloud forest on the Amazonian Flank of the Peruvian Andes, otherwise known as the Peruvian Yungas. The forest was situated on the leeward slope of a large mountain range at 2400 m asl. Due to the uncontrolled illegal trade of orchids in Peru, the exact location is not revealed in order to protect the integrity of the forest. Long-term meteorological data are not yet available from the site. However, a ten-year database (1989-1998) and a different three-year database (2001-2003) that are not calibrated are available from a valley 4 km distance from the study site at 1800 m asl. From the ten-year database, the average annual rainfall is 1293 mm and the average annual temperate is 14.96 °C with a wet season from October until April in most years (Figure 2). The average rainfall from the three-year database is 2302 mm and is considered more accurate[1].

Climatic data were collected from the study site by the author from April 2003 until March 2004. Local farmers and managers were in strong consensus that this period was very dry and warm compared to their conception of the average. During this period, there was 2132 mm of rain and the average temperature was 13.8 °C (Figure 3). From a 3 month calibration period with the valley site, the study site received 1.5 times more rainfall volume, 1.3 times more rain events, and rainfall fell at 1.2 times greater intensity. The temperature average was 2.1 °C lower at the study site. Extrapolation results in an estimated average annual rainfall of c. 2500 - 3000 mm and an average annual temperature of c. 12.8 °C. However, rainfall variability from the region is high (Figure 4) that may be related to the leeward location. During the dry season, mist contacts the canopy at twice the

[1] The 3-year database is currently maintained with calibrated instruments that have not been calibrated to those of the 10-year database. The latter is more useful as a measure of climatic variation than a source of accurate climatic data.

frequency of rain. During the wet season, few days pass without rain and mist is frequent during the day and constant between 9:00 pm and 6:00 am.

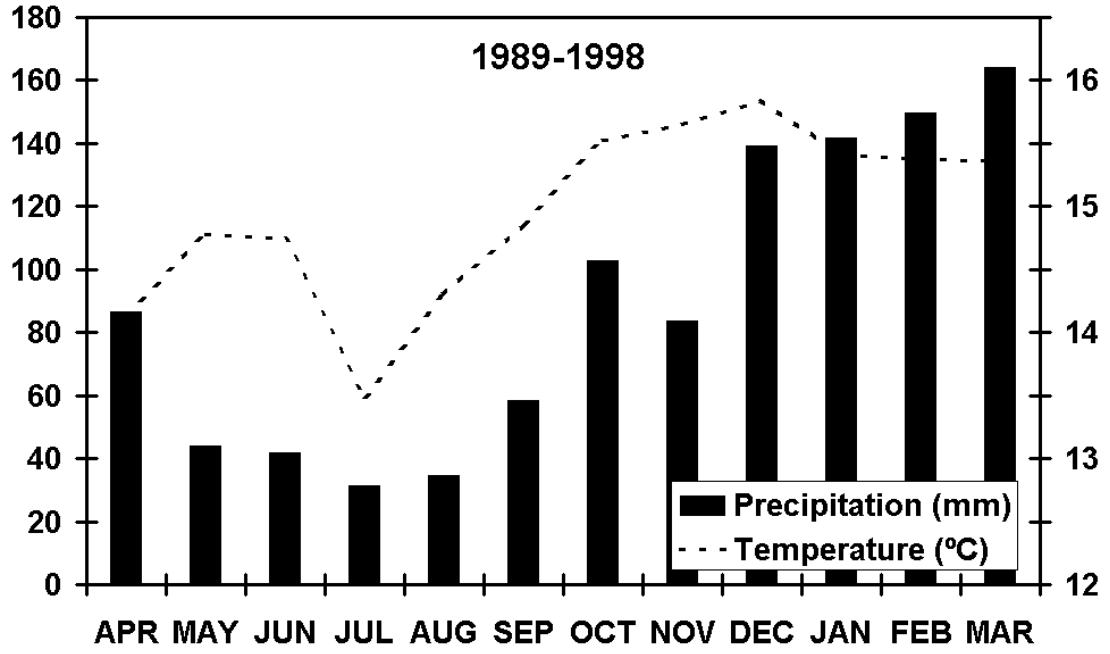


Figure 2: Average monthly precipitation (left axis) and temperature (right axis) at a valley 4 km distance from the study site at 1800 m asl during 1989 – 1998 (data source: SENAMHI).

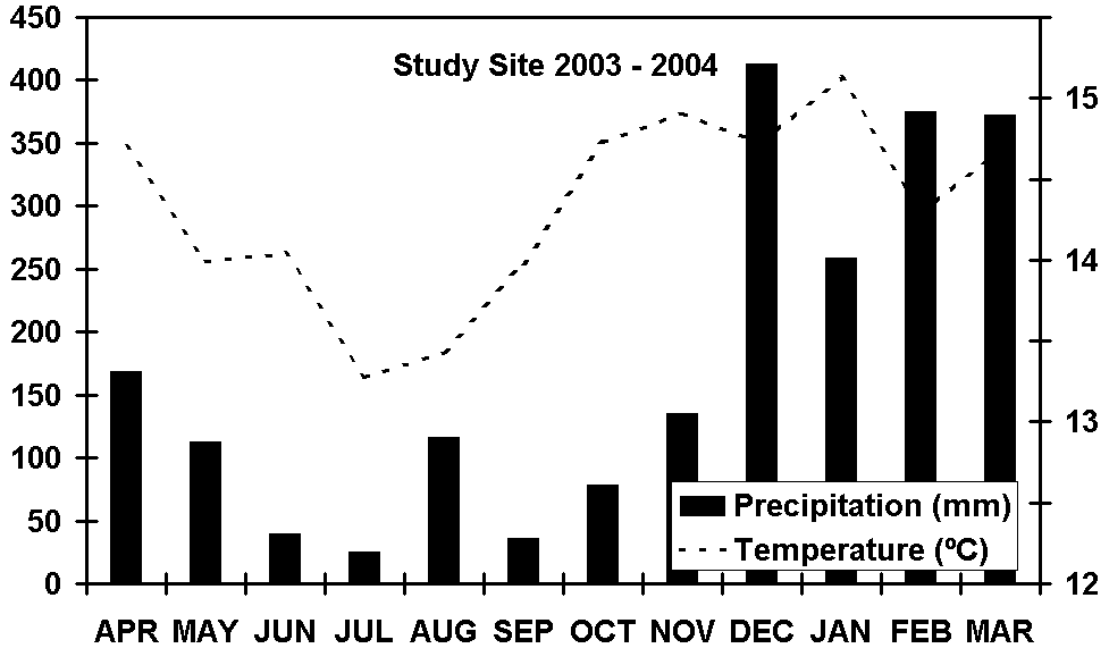


Figure 3: Monthly precipitation (left axis) and temperature (right axis) at the study site at 2400 m asl during the sampling period.

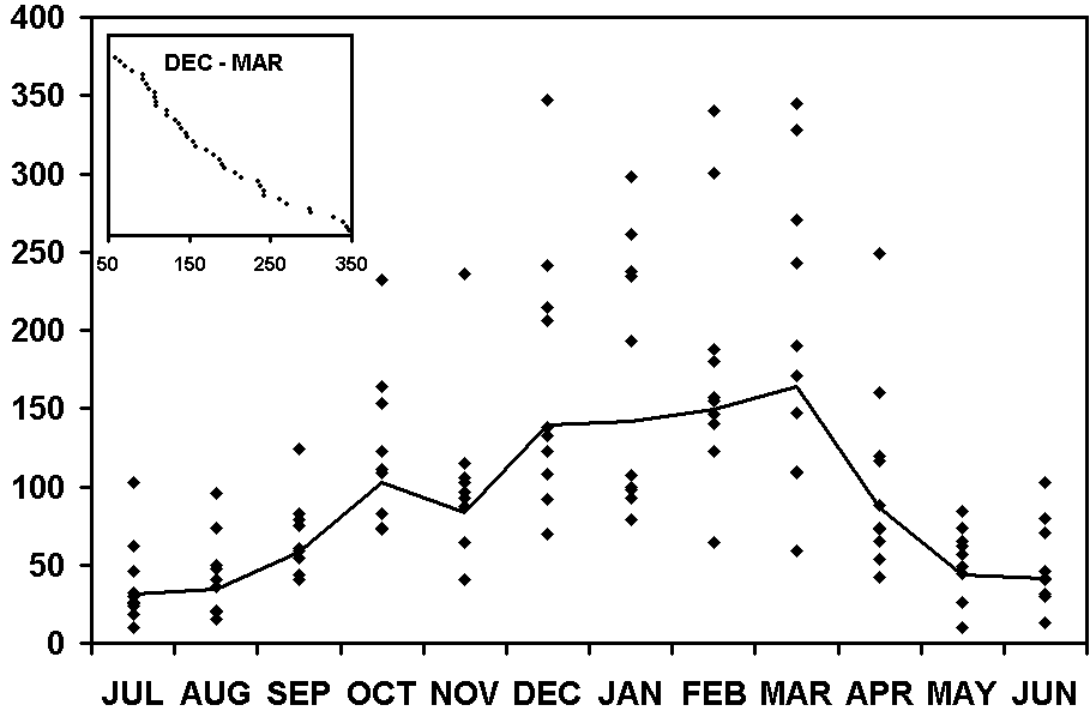


Figure 4: Rainfall variability at a valley 4 km distance from the study site at 1800 m asl during 1989 – 1998. Line indicates the mean. Upper left box shows the distribution of December to March rainfall values. (data source: SENAMHI)

The study site is classified as primary forest (Brack, 1987). Very selective logging may have occurred until 20 years ago for *Cedrela montana* Moritz ex Turcz. and *Podocarpus oleifolius* D. Don ex Lamb., with large (DBH > 2m) individuals mostly removed over 50 years ago (P. Aguilar, pers. com.). The site is located in a steep valley bottom with a westerly aspect. The forest has a dense 15-25 m broken canopy with complex stratification and emergents up to 40 m in height. One study in similar forest recorded a diversity of 154 tree species from 687 individuals (≥ 10cm DBH) from a 1 ha plot (Gómez, 1999; Gómez and Reynel, 2001).

The dominant canopy trees are of the genera *Alchornea* Sw., *Cedrela* P. Browne, *Croton* L., *Escallonia* Mutis ex L. f., *Ficus* L., *Hyeronima* M. Allemão, *Miconia* Ruiz & Pav., *Oreopanax* Decne. & Planch., *Persea* Mill., *Podocarpus* L'Hér. ex Pers., and *Weinmannia* L.. The broken canopy is due to frequent landslides and treefalls that result from high rainfall and very steep slopes (20º - 55º). Frequent earth tremors may also increase landslide frequency (pers. obs.). The understorey is dominated by shrubs and small

trees in the families Ericaceae, Gesneriaceae, Melastomataceae, Piperaceae and Rubiaceae. Tree ferns in the genera *Alsophila* R. Br.*, Cyathea* Sm. and *Dicksonia* L'Hér. are prominent. Epiphytes are dense on most trees. These are dominated by the families Araceae, Bromeliaceae, Dryopteridaceae and Orchidaceae.

2.2 Study Design & Field Data Collection

2.2.1 Canopy Sampling

An individual of *Ficus* species (Moraceae) was selected for sampling, based on the selection criteria of emergent status, suitable quantity of epiphytes and accessibility. A forest emergent was desirable, in order to provide a large sample of the upper canopy community from a variety of microhabitats. The smooth-barked *Ficus* tree selected was on a slope of 30º-45º and at a distance of c. 40 m from a valley stream. The tree had a height of 32 m, a diameter at breast height (upslope) of 1.4 m, and the buttressed trunk leaned at a slight angle of c. 5º (Figure 5). Its major ramifications began at a height of 14 m from the base of the trunk (upslope). Branches emerged from trunks at all angles. Being an emergent strangler fig, the architecture did not conform to a standard architectural model, but resembled the common Rauh's Model (Hallé *et al.*, 1978), with a distinctly plagiotropic influence to middle and lower branch systems.

The epiphyte sampling was conducted *in situ*, using rope access techniques (Barker, 1997; Barker and Sutton, 1997; Perry, 1978b) and techniques from the arborist trade (Dial, 1994; Jepson, 2000). These methods permitted the collection of data and plant material from the entire tree without sawing branches. Epiphyte sampling began in August 2003 and was mostly finished in November 2003. During the wet season, some revisiting of the canopy occurred until March 2004.

The host tree was divided into canopy zones (Figure 6), following the widely used classification system of Johansson (1974). This scheme has been widely used and recommended by epiphyte researchers (Bøgh, 1992; Freiberg, 1996, 1999; Gradstein *et al.*, 1996; Gradstein *et al.*, 2003; Hietz

and Hietz-Seifert, 1995b; Nieder and Zotz, 1998). In the present study, Zone 1 was not considered for two reasons. Firstly, terrestrial species commonly inhabit this zone in montane cloud forest (Bøgh, 1992). Secondly, the diversity of habitat within Zone 1 was large due to trunk buttressing and the slope angle.

Within the host tree, clumps of epiphytes comprised the basic subplot level of sampling. They will be referred to as clumps for ease of discussion. A clump is any group of epiphytes, or a single plant, separated by bark on which vascular plants are absent (Figure 7). Each epiphyte species and individual was recorded. Rhizomatous or clumping patches of one species were counted as one individual, following the method of Sanford (1967).

2.2.2 Plant Identification

In order to identify epiphyte species, a number of herbarium vouchers were collected for each fertile species encountered. However, because the canopy sampling could only be performed safely in all parts of the canopy out of the wet (flowering) season, live plants of all sterile morphospecies were collected. More than 1400 plants were catalogued and placed in a grow house constructed at the study site. Plants were numbered and stored in individual plant pots and watered to encourage flowering. During the wet season the grow house was visited every two days to recover flowers and plant material for herbarium specimens. All herbarium vouchers were photographed for identification with high-resolution macro-images while fresh. Flowers were preserved in 90% alcohol. Herbarium vouchers were deposited (in order of preference with minimum vouchers) at: Selva Central Herbarium (new), Peru (OXA – 2 vouchers); Missouri Botanical Garden, USA (MO – 2 vouchers); Universidad Nacional Agraria La Molina, Peru (MOL – 1 voucher); Universidad Nacional Mayor de San Marcos, Peru (USM – 1 voucher); Universidad Nacional de La Libertad-Trujillo, Peru (HUT – 1 voucher); Universidad Nacional de la Amazónia Peruana, Peru (AMAZ – 1 voucher).

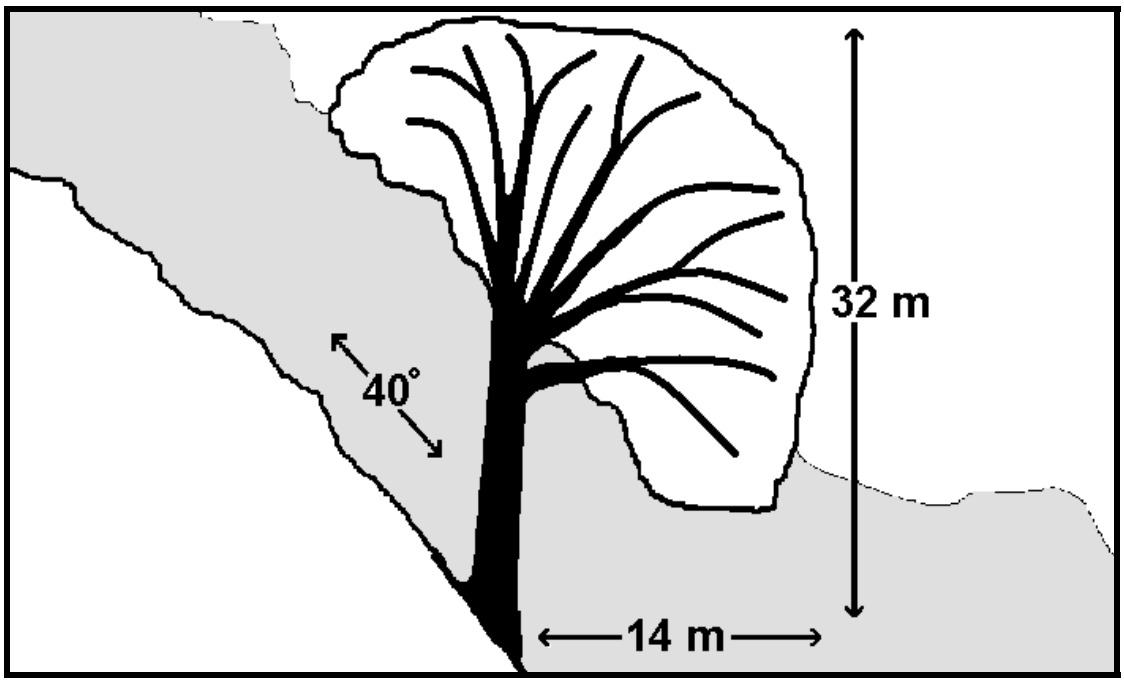


Figure 5: A cross–section of the *Ficus* emergent. Shaded area represents the canopy.

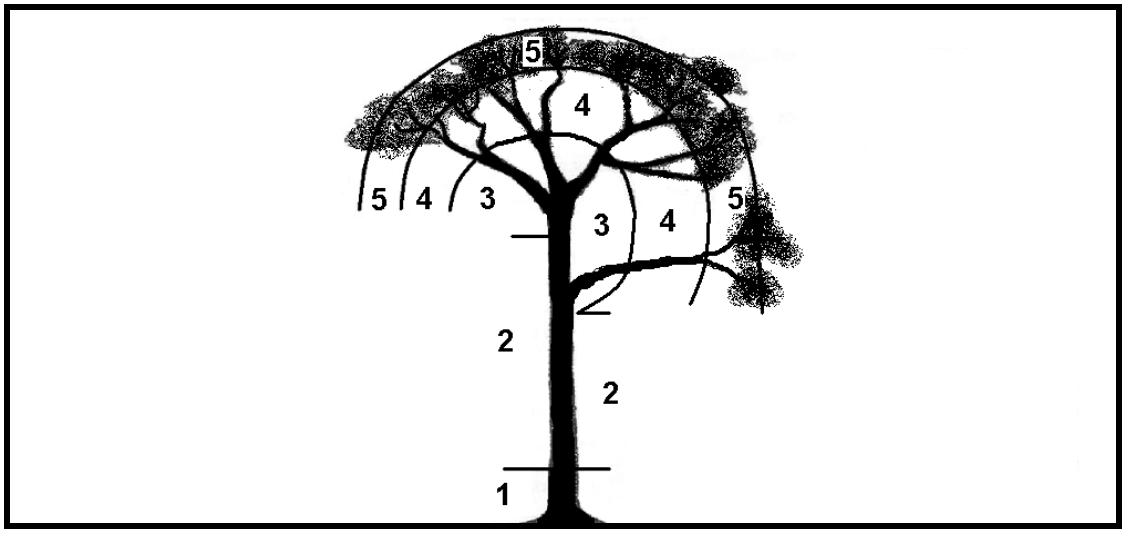


Figure 6: The Johansson (1974) canopy zone classification scheme

Figure 7: Two distinct epiphyte clumps separated by uncolonised bark

Once a suitable number of vouchers/live plants had been collected for a given species, no further collections were made. However, some pleurothallid orchid species were known to have very similar morphologies, so in these cases, specimens were collected in every case in which only fertile specimens could differentiate species. 1528 plants were collected from the canopy from a number of *Ficus* hosts. 570 fertile herbarium vouchers were deposited. Many specimens remain in cultivation to await flowering over the following years, and the identification to species of vouchers is ongoing.

2.2.3 Lifeform and Taxonomic Groups

All species were classified by lifeform (growth habit) and by taxonomic group. The most complete works on the classification of epiphyte lifeforms was by Hosokawa (1943). The lifeform classification in the present study is a modified version of this original classification. The lifeform groups are as follows.

Ascending: a plant where the main stem is erect, plant stems curve upwards from the node

Caespitose: a plant with a tufted growth form where stems arise from a basal node or rhizome

Climber: a plant that climbs and attaches vertically

Closed Tank: a bromeliad with tightly tubular enclosed rosette

Filmy Fern: a filamentous fern group

Lepanthid: a pleurothallid orchid with lepanthiform sheaths

Long Creeping: a fern with a long creeping rhizome

Long Repent: a plant with a long rhizome/stem that spreads along the stem and sends out roots from nodes

Open Tank: a bromeliad with a broadly open rosette

Pendant: a plant that has drooping stems and leaves

Short Creeping: a fern with a short creeping rhizome

Short Repent: a plant with a very short rhizome/stem that spreads along the stem and sends out roots from nodes

Taxonomic groups were as follows.

Aroid: all members of the Araceae

Bromeliad: all members of the Bromeliaceae

Herb: all non-woody dicotyledonous angiosperms

Orchid: all members of the Orchidaceae excluding the subtribe Pleurothallidinae

Pleurothallid: all members of the Pleurothallidinae (Orchidaceae)

Fern: all members of the Polypodiopsida

Woody Dicot: all woody dicotyledonous angiosperms

2.2.4 Environmental Data

Geometric measurements for each clump were the diameter and angle of the branch upon which the clump resided and the canopy zone. In order to track the sampling of the tree, each branch was numbered in an artificial numbering system. Clumps were numbered along each branch section and were assigned a cardinal orientation from the trunk. Due to logistical constraints, no distance measures were made on long branches, just the sequence of clumps.

Meteorological data from above the canopy were needed to determine the microclimate within it. Data were collected for temperature, relative humidity, vapour pressure, Photosynthetically Active Radiation (PAR) and precipitation. Data were recorded at 10-second intervals and averaged at 10-minute outputs on a Campbell Scientific CR10x datalogger. Temperature, relative humidity and vapour pressure were recorded with a shielded Campbell Scientific CS500 temperature/relative humidity probe. PAR was recorded with a LiCor SB-180 quantum sensor. Precipitation was recorded with a Hydrological Services tipping bucket rain gauge with 0.254 mm recording capacity. All instruments and sensors were mounted on an 18 m canopy mast fabricated for the study. The mast was constructed less than

70 m from the study tree, where the quantum sensor obtained an unobstructed sky view.

2.3 PAR & Canopy Structure

Radiation statistics for each clump were obtained from a vertical hemispherical image taken with a NIKON 4500 Coolpix digital camera and a NIKON FC-E8 fisheye lens adapter. The camera has an effective pixel count of 3.87 million pixels (2272 x 1704). Photos were taken under the *FISHEYE 1* setting. The *Image Sharpening* function was used and set to *HIGH*. Exposure settings were set to *–2.0*. Photos were taken using the 10-second timer option to reduce jitter. Images were recorded at the highest compression resolution setting on the camera (*FINE*) and stored as JPEG image files at minimum compression ratios to retain 100% quality. Englund *et al*. (2000), recommended the low-resolution setting to reduce storage file size. Their recommendation is not advocated here and should not be followed by anyone with the capability to store images at high resolution. Digital images have lower definition under some conditions compared to film imagery (Frazer *et al.*, 2001), and these inaccuracies are exacerbated with low quality images. Images were aligned north in the field using a hand held compass. To level the camera in the canopy, a custom-built aluminium hand held camera mount with two perpendicular horizontal spirit levels was used. Where possible, in each canopy section, canopy sampling proceeded from the ground up so that small disturbances/removal of voucher specimens did not affect sky values obtained from the vertical hemispherical images.

Radiation and canopy structure data from hemispherical images was produced using the hemispherical image analysis program HemiView (Delta-T Devices Ltd., 2001). There were two stages to the image adjustment before analysis could proceed. Firstly, all images needed to be corrected for light coloured objects within the canopy below the horizon. Being in a mountainous valley, mountain ridges defined the horizon and affected direct radiation significantly (Figure 8). Photos were taken on different days over a range of conditions. Under some conditions, tree trunks and vegetation below the

horizon were over-exposed so that they appeared very light in colour. To correct this error, all 606 images were masked with a Horizon Template image that defined the outline of the horizon from the tree. This mask retained the position of the hemisphere, but blacked out all vegetation lying below the horizon in order to standardise all images (Figure 8).

Figure 8: (left) Original Hemispherical images and (right) masked hemispherical images

Secondly, images were gray-scale classified using HemiView to correct for different exposure levels. Prior to the classification, a set of 20 images was selected. On two consecutive days with files in a different order, images were classified and analysed using HemiView to gauge the level of bias. The values from the two days had a Pearson correlation coefficient of 0.97. For the following three days over a combined 48-hour period, all 606 images were classified, aligned and saved as HVS files (HemiView Settings File) for later analysis (c. 4.5 minutes per image). Due to time restrictions, the process could not be repeated as suggested by Hale and Edwards (2002).

The HemiView program calculates radiation statistics generated from a solar model that can be determined from real data. One year of PAR data from the site, and, a diffuse/global radiation dataset from Hobart were used to create a solar model for the program. The solar model requires both transmitivity and a diffuse proportion from the site. The resulting analysis of 12:00pm – 12:30pm PAR data (not shown) gave a yearly average transmitivity of 0.39 at the site. A relationship between diffuse and global radiation was

derived from the Hobart dataset and used to determine diffuse radiation from the tropical latitude of the site with an equation calculated for the Peruvian site (y = 0.3568x + 0.1581)(Iqbal, 1983). The diffuse proportion was determined to be 0.57 at the site. The HemiView model assumes a circular orbit and a solar constant of 1370 Wm^{-2}. This is approximately equal to 2900 umol m^{-2} s^{-1} that is used in the solar radiation model. The solar model used the *Uniform Overcast Sky* setting (Steven and Unsworth, 1980). Latitude, longitude, altitude above sea level and magnetic declination of the study site were also given to the program to calculate the sun's path over the hemispherical image. The manufacturers specifications of lens distortion used by HemiView had been previously shown to be sufficient (Frazer *et al.*, 2001) and were used without modification.

2.3.1 Output Descriptions

HemiView generates data outputs from each hemispherical image based on an overlaid azimuth and zenith skymap. Three HemiView outputs generated were ***VisSky***, ***TotBe*** and ***LAIDev***. These outputs are not correlated. Three additional diurnal periods, were calculated manually from a monthly 30-minute below canopy direct radiation output sheet, included ***RadMorn***, ***RadMidd*** and ***RadAft***.

VisSky: The proportion of visible sky not obstructed by vegetation or topography. It is reported as a fraction.

TotBe: The total PAR encountered at the site. It includes the total of both direct and diffuse radiation reported in moles (mol m^{-2} yr^{-1}).

LAIDev: The measure of uniformity of the ellipsoidal Leaf Area Index (LAI) distribution (Campbell, 1986) between skymap sections. It is an index of canopy (obstruction) evenness. It is calculated as the root mean square deviation of LAI in each skymap section (Equation 1).

RadMorn: The Direct PAR from 5:46am – 9:45am encountered at the site reported in moles (mol m^{-2} yr^{-1}).

RadMidd: Direct PAR from 9:46am – 1:45pm encountered at the site

reported in moles (mol m^{-2} yr^{-1}).

RadAft: Direct PAR from 1:46pm – 5:45pm encountered at the site reported in moles (mol m^{-2} yr^{-1}).

Equation 1: The calculation of LAIDev (Delta-T Devices Ltd., 2001)

$$LAIDev = \frac{(LAI_{\alpha,\theta} - LAI)^2 . nAzim . nZen . SolidAng_{\alpha,\theta} . SkyValid_{\alpha,\theta}}{(nAzim.nZen - 2) \sum_{(\alpha,\theta)} SolidAng_{\alpha,\theta} \; SkyValid_{\alpha,\theta}}$$

Where:

LAIDev is the LAI deviation

$LAI_{\alpha,\theta}$ are the values of LAI by skymap sector.

LAI is the overall canopy LAI.

nAzim is the number of azimuth divisions in the skymap.

nZen is the number of zenith divisions in the skymap.

$SolidAngle_{\alpha,\theta}$ is the angular size of the sector.

$SkyValid_{\alpha,\theta}$ is the proportion of valid (not ignored) pixels in the sector.

The "-2" in the denominator is because this is only a sample of the canopy, and two degrees of freedom have been used already in calculating the overall LAI values.

Chapter 3 Structure and Composition

3.1 Aims

This chapter describes the floristic composition of the *Ficus* epiphyte community in order to accomplish the first research aim.

1. Determine the structure and flora of the epiphyte community on a single *Ficus* host tree in comparison to other trees and forests

This aim is achieved by identifying the complete epiphyte flora of an individual *Ficus* host, investigating many taxonomic and structural aspects of the flora, and comparing these results to those found within other similarly investigated trees and, where applicable, in other forests. The taxonomic and structural investigations of the whole tree were aided by analysis of individual epiphyte clumps and the distribution of epiphyte lifeforms and taxonomic groups within the flora.

3.2 Methods

All species and all individuals of epiphytes were recorded from a single *Ficus* species host. These were identified taxonomically and to lifeform groups. Alpha diversity was reported with a variety of common diversity statistics including the Fisher's-Alpha Index (α) (Fisher *et al.*, 1943), the Shannon Weaver Index (H') (Shannon and Weaver, 1949) and the Simpson's Index (D) (Simpson, 1949) (Equation 2).

Two Species Area Curves were calculated using a randomised collection sequence (10 randomisations), and, a Sørenson distance matrix within PC-ORD (McCune and Mefford, 1999). Species richness estimations were calculated using first- and second-order jackknife estimators with non-parametric resampling procedures (Burnham and Overton, 1979; Heltshe and Forrester, 1983; Palmer, 1990, 1991) in PC-ORD (McCune and Mefford, 1999). To display trends in clump abundance and richness, clump abundance scores were aggregated into groups of three in rank order (1-3, 4-6, 7-9,.....),

and clump richness scores were aggregated into groups of two in rank order. Non-linear regression analysis of clump composition values was performed with SigmaPlot (SPSS Inc., 2001).

Equation 2: Alpha diversity measures

$$S = \alpha * \ln(1 + n/\alpha)$$

$$H' = -\sum_{i=1}^{n} P_i \log P_i$$

$$D = 1 - \sum_{i=1}^{n} P_i^2$$

where: *S* is number of taxa, *n* is number of individuals, α is the Fisher's Alpha, P_i is the importance probability in species *i* , H' is the Shannon-Wiener Diversity Index and D is the Simpson's Index. *P* is relative to clump richness/abundance totals (see Greig-Smith, 1983; based on Shannon and Weaver, 1949)

3.3 Results

3.3.1 Floristic Composition

One hundred and ninety holoepiphyte species and 5 hemiepiphyte species comprising 9022 individuals in total were found within 632 clumps of vascular epiphytes recorded on the tree. All hemiepiphytes were at the epiphytic stage of their life. All vascular epiphyte taxa recorded are listed in Appendix I with their lifeform, percentage frequency within epiphyte clumps, and percentage abundance of all individuals. These species came from 51 genera of 15 families (Table 1). Eighty-five species came from just 5 genera (Appendix I). The Orchidaceae dominate the numbers of genera, species and individuals.

The distribution of lifeform and taxonomic groups within the vascular epiphyte flora is summarised in Table 2 and Table 3 respectively. The caespitose lifeform represented the largest number of species. The long repent and open tank lifeforms represented the largest proportion of individuals. All of the previously mentioned lifeforms were also well represented within the clumps. The pleurothallid group represented the largest

proportion of species. They account for 37% of all species, 25.5% of all individuals and occur in 72.8% of clumps. The bromeliad, orchid and pleurothallid groups represented the largest proportion of individuals. All of the previously mentioned groups and the fern group were well represented within the clumps.

Table 1: Summary of the vascular epiphytes families found in the Ficus host

Family	Genera	Species	Individuals
Araceae Juss.	2	3	23
Araliaceae Juss.	1	1	2
Aspleniaceae Newman	1	2	11
Bromeliaceae Juss.	3	17	2275
Crassulaceae J. St. Hil.	1	1	1
Ericaceae Juss.	3	9	430
Grammitidaceae Ching	5	10	322
Hymenophyllaceae Link	1	2	24
Lomariopsideae Alston	1	12	807
Orchidaceae Juss.	23	114	4806
Oxalidaceae R. Br.	1	1	3
Piperaceae C. Agardh	2	6	114
Polypodiaceae Bercht. & J. Presl	4	8	43
Rubiaceae Juss.	1	1	25
Vittariaceae (C. Presl) Ching	2	2	7
Undetermined		6	129
TOTAL 15	**51**	**195**	**9022**

Table 2: Summary of lifeforms found within the epiphyte flora

Lifeform	Species (%)	Individuals (%)	Clumps (%)
Ascending (Asc)	21.0	5.1	38.8
Caespitose (Cae)	28.2	19.6	66.7
Climber (Clb)	3.6	0.4	4.0
Closed Tank (CTa)	2.1	0.2	2.1
Filmy Fern (FF)	1.0	0.3	1.7
Lepanthid (Lep)	8.2	1.4	7.3
Long Creeping (LCr)	5.6	4.2	24.8
Long Repent (LRp)	6.2	23.4	69.8
Open Tank (OTa)	6.7	25.4	71.5
Pendant (Pnd)	4.1	1.1	10.1
Short Creeping (SCr)	10.3	9.6	58.1
Short Repent (SRp)	3.1	9.3	45.7

Table 3: Summary of classes found within the epiphyte flora

Taxonomic Group	Species (%)	Individuals (%)	Clumps (%)
Aroid	1.5	0.2	2.5
Bromeliad	8.7	25.8	71.8
Herb	5.6	1.4	13.7
Orchid	21.0	27.9	74.4
Pleurothallid	37.4	25.9	72.8
Fern	19.0	13.7	64.4
Woody Dicot	6.7	5.0	45.2

3.3.2 Community Structure

The species richness of the vascular epiphytic flora of the tree was 195. The α was 35.11, the H' was 3.45 and the D was 0.93. Two species, Bromeliaceae sp. 2 and *Maxillaria notylioglossa*, represented c. 30% of all individuals. Only 14% of species (28 spp.) were found in 5% or more of the clumps. Thirty-nine percent of species (77 spp.) were found in only one clump and 11% (21 spp.) were found in only two clumps. Thirty percent of species (59 spp.) were represented by only one individual and 10% (20 spp.) were represented by only two individuals.

Both the species area curves generated for the epiphyte community using the randomised (Figure 9) and distance matrix (Figure 10) methods indicated only a small amount of levelling. The first-order jackknife estimate was 271.9 species and the second-order jackknife estimate was 327.7 species. The dominance/diversity abundance curves showed a lognormal distribution (R^2 = 0.96) that describes dominance by few species, with many species of intermediate abundances (Figure 11). There is an unusually large proportion of rare species.

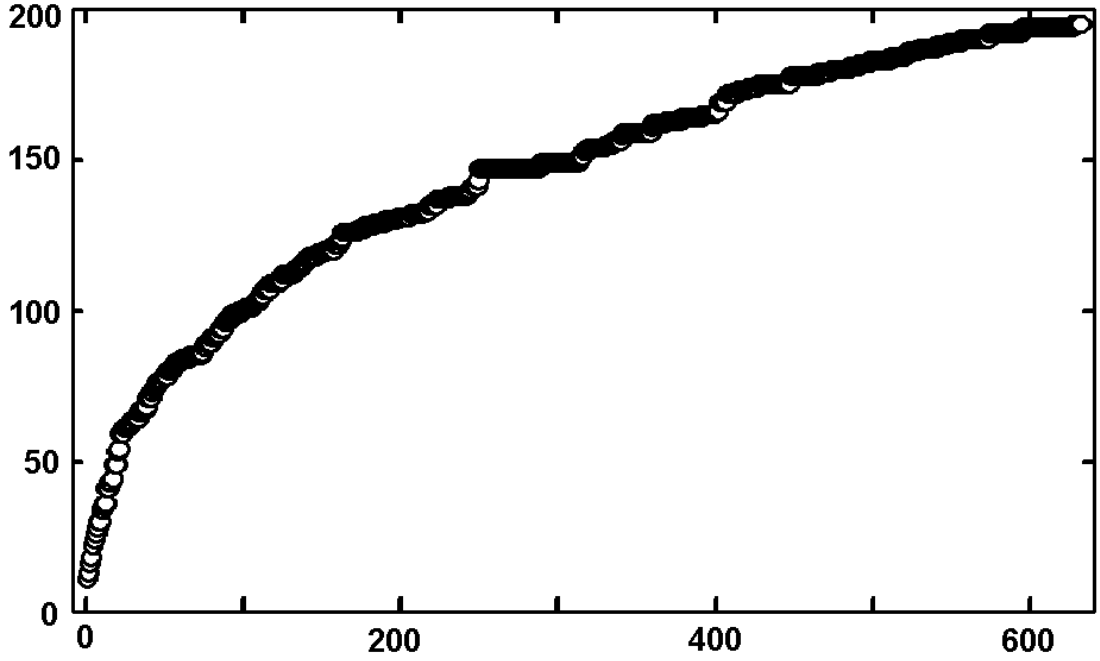


Figure 9: Species Area Curve of the *Ficus* epiphyte flora using a randomised order. The accumulated number of species (Y) is plotted against the number of clumps (X).

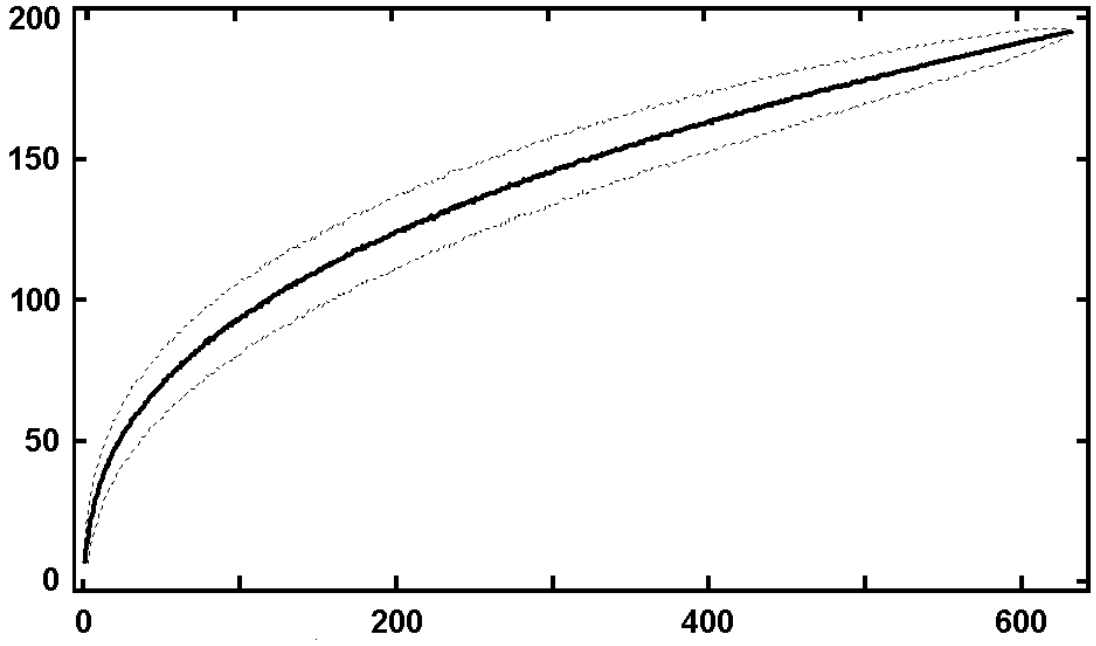


Figure 10: Species Area Curve of the *Ficus* epiphyte flora using a Sørenson distance matrix. Average accumulated number of species (Y) is plotted against the number of clumps (X). Dotted lines represent ± 1 standard deviation

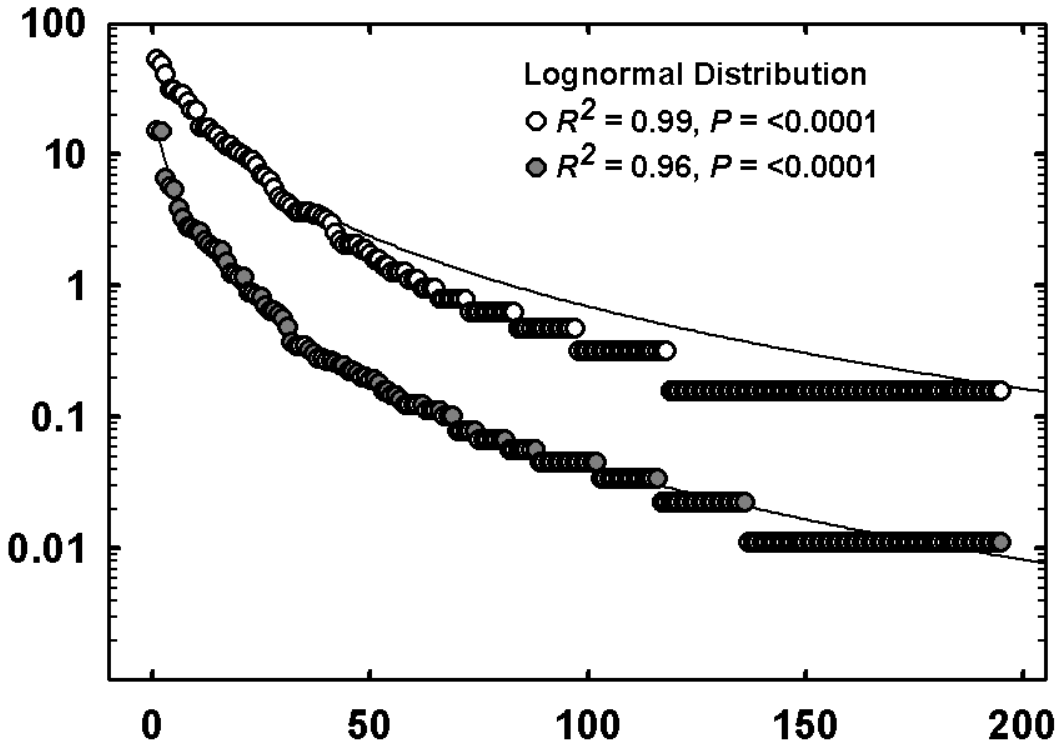


Figure 11: Dominance/diversity curves for the total epiphyte flora. Percentage abundance with the tree (open circles) and percentage frequency within clumps (shaded circles) on a log scale (Y) of all epiphyte species in rank order of abundance/frequency (X).

3.3.3 Epiphyte Clumps

The distribution of species frequency within clumps followed a lognormal distribution (R^2 = 0.99)(Figure 11). The richness and abundance of vascular epiphytes within the clumps had a wide range (Figure 12). There is a moderate relationship between the clump richness and abundance (R^2 = 0.615, P = 0.000). The frequency of both clump abundance and clump richness followed non-linear patterns. The aggregated frequency groups of clump abundance (Figure 13) best fit a Pseudo-Voigt peak distribution (R^2 = 0.99). The aggregated frequency groups of clump richness (Figure 14) best fit a Pseudo-Voigt peak distribution (R^2 = 0.98). The modal clump abundance was 7-9 individuals and the mean was 14.08 individuals. The modal clump richness was 5-6 species and the mean was 6.5 species. The average number of individuals of the most abundant species in each plot was 5.31. The clump average alpha diversity score was α = 6.19 (highest α = 61.14), H' = 1.48 (highest H' = 2.93) and D = 0.68 (highest D = 0.93). All lowest values

were zero. Species richness within aggregated clump abundance groups best fit a Weibull distribution (R^2 = 0.92) (Figure 15).

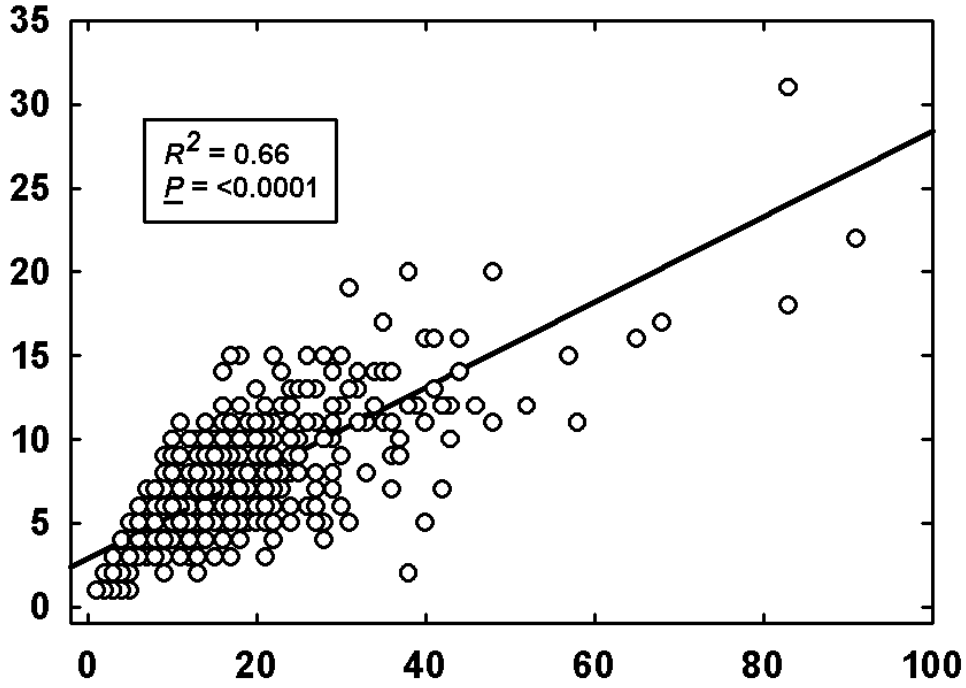


Figure 12: The species richness (Y) and abundance of individuals (X) within vascular epiphyte clumps

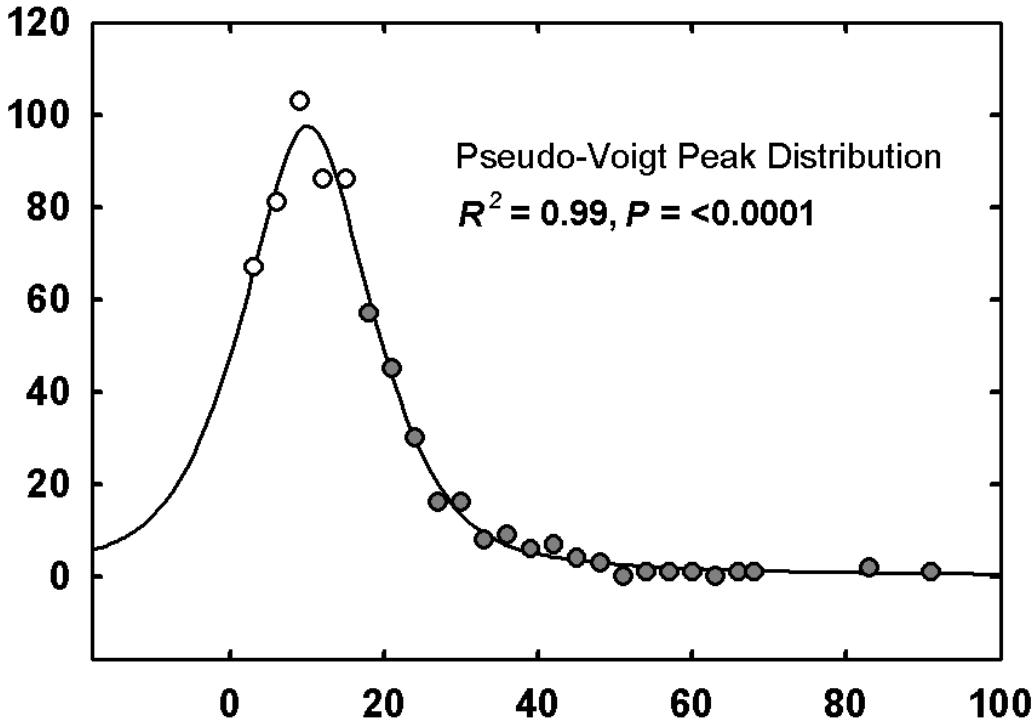


Figure 13: The frequency (Y) of aggregated clump abundances (X). Small clumps (open circles) and large clumps (shaded circles).

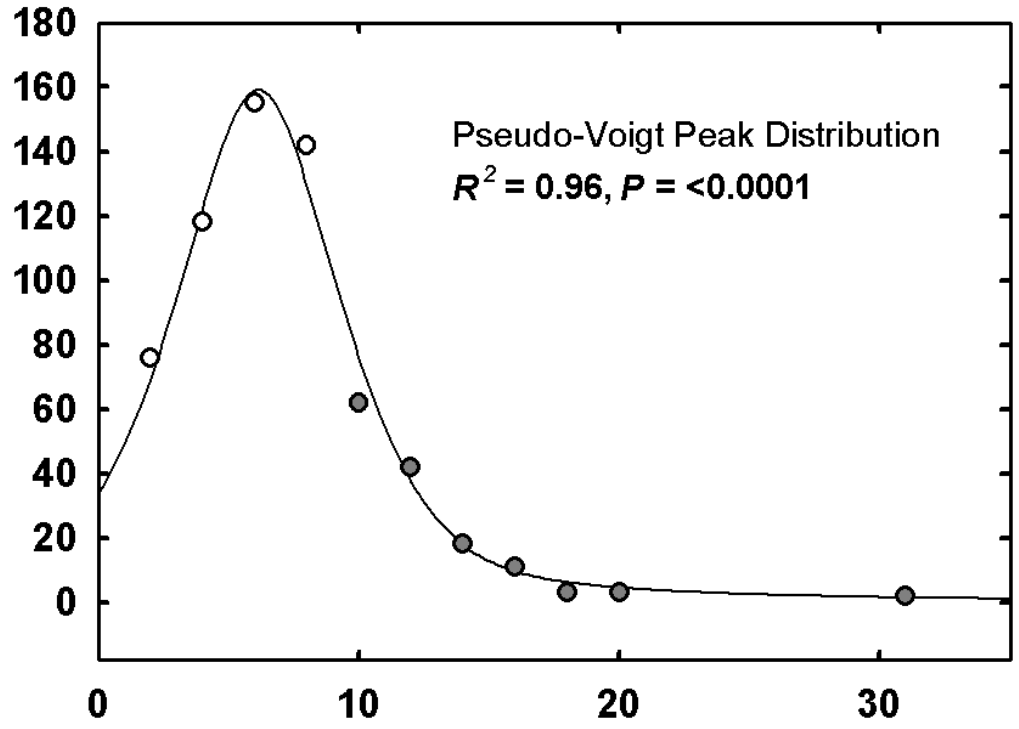


Figure 14: The frequency (Y) of aggregated clump richness (X). Low richness clumps (open circles) and high richness clumps (shaded circles).

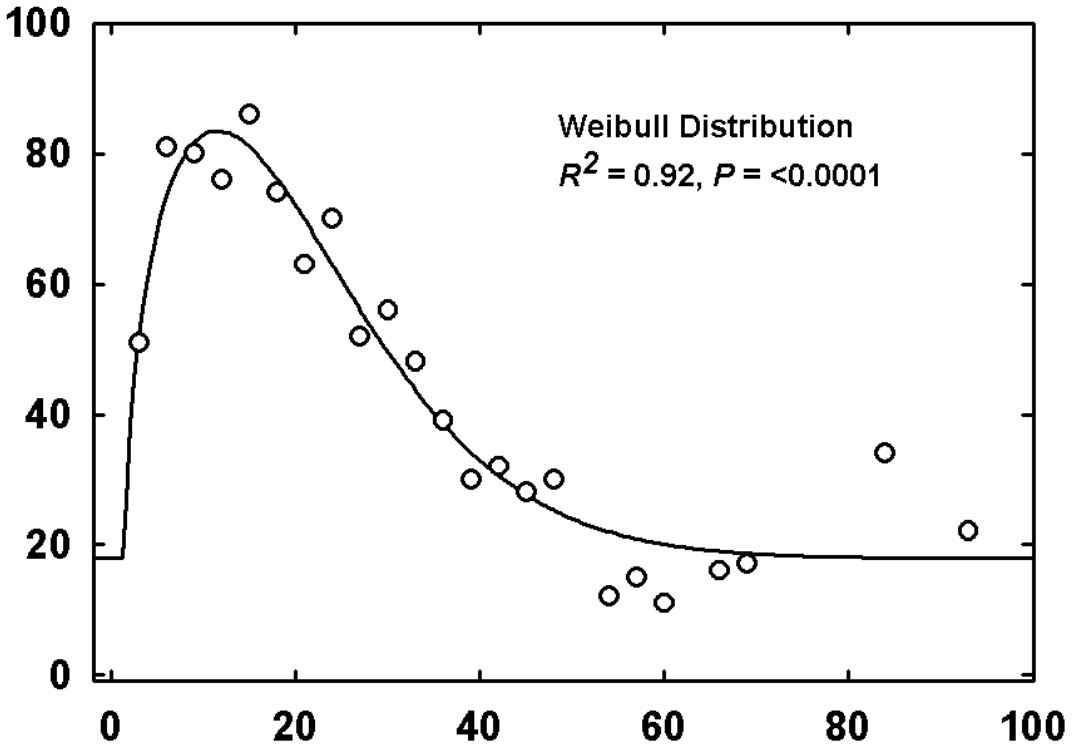


Figure 15: The species richness (Y) within aggregated clump abundance groups (X).

3.4 Discussion

3.4.1 Floristic Composition

The floristic composition of the epiphyte community is similar to those found in other species rich neotropical montane areas (Bøgh, 1992; Bussmann, 2001; Engwald *et al.*, 2000; Ingram *et al.*, 1996). The total dominance of the Orchidaceae is a uniform trend in mesic tropical epiphyte communities. The prominence of Bromeliaceae is also a very common feature. Other features shown that are typical of neotropical epiphyte communities include the diversity of ericaceous epiphytes and hemiepiphytes, the diversity of the *Elaphoglossum*, the Grammitidaceae ferns, and the Piperaceae.

The abundance of lifeforms was heavily influenced by the two most abundant species, Bromeliaceae sp. 2 (open tank) and *Maxillaria notylioglossa* (long repent). The open tank lifeform of the Bromeliaceae is particularly well-adapted to an epiphytic role in mesic environments by its capacity to trap and store moisture. The long repent lifeform of *Maxillaria notylioglossa*, allows plant stems to search for light whilst retaining an original attachment, an effective local colonisation mechanism. The abundance of this lifeform was also reported by Freiberg (1996). However, there were a low number of species, which suggests that these species occupy a niche for which there is some competition. The more species rich ascending lifeforms occurred in a large number of clumps, but had a very low abundance. These plants are generally large and long-lived, so abundance is not critical to the survival of the species. The caespitose lifeform was particularly species rich and abundant. Many of the species vegetatively reproduce, forming dense clumps that secure the community for many years and increase the probability of recruitment over time.

The pleurothallid orchids are the most dominant single group of epiphytes. The figures presented are twice the diversity and two thirds of the density found 2900 m asl in Ecuador by Bøgh (1992). Pleurothallid orchids generally have a caespitose or short repent habit (Luer, 1986b). They are

wind dispersed, having tiny dust seeds like many other epiphytic orchids. They are mostly pollinated by Diptera (flies). A high species richness of the Pleurothallidinae in neotropical montane epiphyte floras is common phenomenon (Bøgh, 1992; Bussmann, 2001), though in the present study the species richness is above the normal range.

3.4.2 Community Structure

A prominent feature of the community structure was dominance by a few species and the high contribution to species richness by low abundance species. This was evident by the low number of species (14%) occurring in $\geq$ 5% of the clumps. Freiberg (1999) found that 33% of epiphyte species occurred in $\geq$ 5% of the plots. However, those plots were large and geometrically defined (1 m^2) making a comparison difficult. The 9000+ individuals from a single tree found in the present study is much greater than other published figures known to the author (1001 - Barthlott *et al.*, 2001; 505 - Pupulin *et al.*, 1995).

Each index of alpha diversity describes some features of community structure better than others. For that reason, a number of different measures are presented here that each describes particular attributes of community structure. The value of α is a common alpha diversity measure for tropical forest sites due to the low influence of sample size. This, and its calculation only from totals of richness and abundance, makes it ideal for the comparison of different sites. α makes no allowance for the abundance of species within the community. The α from the present study (α = 35.11) is higher than: the montane 175 m^2 plot of Bøgh (1992) (α = 28.77); the montane 0.1 ha plot of Engwald *et al.* (2000) (α = 23.12); the montane single tree of Barthlott *et al.* (2001) (α = 15.86); the lower montane single tree (only orchids) of Pupulin *et al.* (1995) (α = 9.86); and the lowland 1.5 ha plot of Engwald *et al.* (2000) and Nieder *et al.* (2000) (α = 12.86).

Despite an abundance of epiphyte studies, only those listed above have published numbers of both species and individuals necessary to calculate α. Comparisons with plot studies require some consideration of collection area. In plots, a higher percentage of species would be expected

to come from the understorey compared to single tree studies. In single trees, only one trunk is sampled in the understorey relative to the large upper canopy area. Therefore, it would be expected that plot studies, which include whole trees, a higher diversity of species should be found. In light of this consideration, the flora of the *Ficus* host appears to be very diverse.

The α of the flora of the *Ficus* host was only moderately high when directly compared to the α of the tree species in the forest (α = 62.96). The tree community is an exceptionally rich montane site, but is far from the most diverse tree community (Yanamono, Peru, α = 235.67). This highlights the structural differences between diverse epiphyte and tree communities.

The value of D, often considered a measure of dominance, is influenced by the species of high abundance. The *Ficus* host displayed an extremely high diversity by this measure (D = 0.93). This was initially surprising given the dominance of the total abundance by a few species of the tree (5 spp - 47.72% of individuals). The only values of D for other epiphyte communities available are those calculated with biomass by Hietz and Hietz-Seifert (1995a) for a range of forest types. These are much lower than those in the present study (D=0.1-0.54).

The H', a measure of evenness, influenced by less abundant species, shows a high value (H' = 3.45) that illustrates the high diversity amongst lesser abundant species. This was higher than that found in montane forest by Barthlott *et al.* (2001) (H' = 3.15). Again, the range of biomass abundance H' was reported by Hietz and Hietz-Seifert (1995a) (H'=1.11-2.7) that was again much lower than that of the present study, suggesting that structural interpretation from biomass abundances might differ from those based on density.

The dominance/diversity curve shows the general lognormal distribution of species (Figure 11) that would be expected given the large assemblage. Lognormal distributions generally represent mature communities where species are persistent (Magurran and Henderson, 2003). The majority of the curve follows the typical lognormal distribution, which may indicate the community is non-equilibrium (Hubbell, 1979). However, at the bottom of the

curve, the abundance of rare species appears larger than what is typically predicted by a general lognormal distribution where the rarest species decline in frequency rapidly. This was also found in an estuarine fish community by Magurran and Henderson (2003). This anomaly is likely to be a signature of the species rich population and the high abundance of canopy species with sparse and sparsely clumped distributions. The abundance of such distribution patterns is becoming increasingly apparent from more detailed epiphyte distribution studies (Ackerman *et al.*, 1989; Nieder *et al.*, 2000; Nieder *et al.*, 2001; Tremblay, 1997). It appears that the community is rich, very heavily dominated by a few species, yet rather evenly distributed throughout the rest of the lesser abundant species (though there are little data with which to compare)..

Overall, with the exception of alpha diversity, there is little evidence to suggest that these general structural characteristics are qualitatively different to other neotropical epiphyte communities.

3.4.3 Epiphyte Clumps

Within the tree, epiphyte clumps showed a wide range of density and diversity values. Following the distribution of the species abundance within the complete flora, species frequency within clumps showed a near perfect lognormal distribution that typifies a large mature population. The analysis of the clump composition showed the moderate positive relationship between species richness and abundance within clumps. There is an interesting non-linear trend observed in the frequency of both clump abundance (Figure 13) and clump richness (Figure 14). The community structure is characterised by a large number of low to medium abundance clumps, which could be partly explained by a predominance of recent establishment.

However, such a successional trend may explain a normally distributed non-linear curve, but it does not alone explain the strong peak distributions in both clump richness and clump abundance. From 13-15 to 16-18 abundance groups, and from 7-8 to 9-10 species groups, there is a significant drop-off in value. There appears to be non-symmetry in the peak curves, especially in the richness group (Figure 14). This slightly non-symmetrical element to the

distribution suggests there is a mechanism that interrupts the natural succession of the community by significantly reducing the clump frequencies past an abundance/richness threshold. This mechanism may be epiphyte slumping, whereby after a period of growth, epiphyte clumps pass a threshold beyond which they become very easily dislodged when waterlogged due to a weight-attachment imbalance. Clumps of a small size have a good weight to attachment ratio and are not markedly affected by slumping. Clumps that pass a threshold in their weight-attachment ratio and are affected by slumping. A similar mechanism was found in cliff dwelling communities (Coates and Kirkpatrick, 1992). Furthermore, the *Ficus* hosts are one of the principal wet season food sources for the brown woolly monkey *Lagothrix lagotricha* Humboldt. These tenacious canopy mammals were observed crashing their way through Ficus species on a daily basis from November until March and appeared an undoubtable source of canopy disturbance.

Epiphyte slumping has been widely postulated from general observations (Freiberg, 1996; Perry, 1978a). Hietz (1997) also used photo evidence to determine the mortality rates of individual epiphyte species from branch fall or other than branch fall (believed to be mostly slumping). The former, being habitat loss, is not related to epiphyte slumping. The results from the latter, assumably from slumping, are difficult to compare to the present study as they deal with individual species on branches where humus deposits were thin and on fissured bark. The latter suggests that the stability of individuals is independent of surrounding individuals. However, he did find that species of *Tillandsia* (Bromeliaceae) was worse affected by slumping at a smaller size and larger branch diameters that will be revisited below. From the present study, where epiphytes within clumps are inextricably linked by the root bound humus accumulations, it appears that we now have quantitative evidence of the existence of a slumping-risk threshold in humus dependant epiphyte communities.

The slumping mechanism could influence the diversity of epiphyte communities. The Weibull distribution of species amongst clump abundance groups (Figure 15) is evidence of this possibility. Weibull distributions are commonly associated with trends where the rate of death/failure/decay etc.

increases with time/age (Smith, 1993). The trend of high species richness at smaller clumps, suggests that maintenance of a dynamic element in epiphyte communities can help to maintain high diversity.

3.4.4 Community Comparison

The species richness found in the *Ficus* host is unprecedented from a single tree and is almost double the highest richness previously reported in the world (Table 4). This could be partly a result of the thorough sampling used in the present study. However, this is not the first study to use grow house techniques to recover fertile plant specimens. Thus, the tree houses an exceptionally rich vascular epiphytic flora.

Table 4: Vascular epiphyte species richness from single trees throughout the world

Richness	Altitude (m asl)	Location	Source
195	2400	Peru	Present Study
109	2000	Ecuador	(Nowicki, 1998)
107	160	Mexico	(Valdivia, 1977)
74	45	French Guiana	(Freiberg, 1999)
66	2200 – 2600	Venezuela	(Barthlott *et al.*, 2001)
65	200	French Guiana	(Freiberg, 1996)
54	1800	Ecuador	(Freiberg and Freiberg, 2000)
51	1780 – 2000	Ecuador	(Rudolph *et al.*, 1998)
45	Unknown	Zaire	(Biedinger and Fischer, 1996)
39	1350	Costa Rica	(Pupulin *et al.*, 1995)
24	1500	Costa Rica	(Ingram *et al.*, 1996)
22	800	West Africa	(Johansson, 1974)
21	465	Jamaica	(Kelly *et al.*, 1994)
21	80	Brazil	(Kersten and Silva, 2001)
20	Unknown (low)	Nigeria	(Sanford, 1967)
12	100	Venezuela	(Nieder *et al.*, 2000)
11	100	Malaysia	(Kiew and Anthonysamy, 1987)

Kelly *et al.* (1994) suggested that within epiphyte rich montane forests, valleys with taller trees would likely reduce epiphyte habitat and diversity relative to ridges. The results here revoke this assumption. The species richness presented in the present study represents a much smaller area than an entire forest or 1 ha plot. However, as will be shown, it is representative of what may be one of the richest epiphyte floras in the world. Including collections by the author outside of the present study during the sampling

period , a total of 257 species of vascular epiphytes, including 159 species of epiphytic orchids were identified from the study area. This collection was restricted to three *Ficus* trees, fallen epiphytes encountered on trails and easily accessible trunks and treefalls near to trails. Despite the incompleteness of the survey, this is the highest richness of epiphytic orchids recorded from any forest in the world (153 - Bussmann, 2001; 96 - Engwald *et al.*, 2000; 109 - Gentry and Dodson, 1987b; 92 - Ingram *et al.*, 1996). Moreover, with the only exception being the extensively collected Ecuadorian region (153 species - Bussmann, 2001), the single tree holds more epiphytic orchids (114 species) than any thoroughly inventoried forest. The complete vascular epiphytic flora might include a third or a half as many more species, as suggested by the species area curve and the jackknife estimates from the single tree, and the known diversity of other hosts and bark substrates within this forest type (Gómez, 1999).

The species area curve generated for the tree (Figure 10) suggested that the single tree was not entirely representative of the *Ficus* epiphyte flora with first-order jackknife estimates suggesting c. 270 species. The second-order jackknife estimate was c. 320 species. Epiphyte host specificity must also be considered. There is a wealth of studies showing host specificity of epiphytes in a range of forest types including this one. Such studies have shown or suggested host specificity due to a range of factors such as bark moisture retention properties, attachment stability, bark substances inhibitory to germination and a range of species specific relationships (Ackerman *et al.*, 1989; Callaway *et al.*, 2002; Frei, 1973, 1976; Frei and Dodson, 1972; Kernan and Fowler, 1995; Kiew and Anthonysamy, 1987; Merwin *et al.*, 2003; Migenis and Ackerman, 1993; Nicolai, 1986; Tremblay *et al.*, 1998; Zimmerman and Olmsted, 1992; Zotz and Vollrath, 2002). Other abundant genera such as *Podocarpus* and *Cedrela,* have fissured bark and different growth cycles. Therefore, there are likely to be some epiphyte species that do not occur on *Ficus* due to bark substrate alone (especially in the un-sampled upper canopy of other genera, pers. obs.). A conservative estimate of vascular epiphyte species richness within the study area is likely to be between 350-400 species.

Such a site estimate, and the data recorded from the study tree, contradicts the generalisations on the distribution of vascular epiphyte diversity made by some authors. Gentry and Dodson (1987b), based on the few datasets available at the time, believed that local epiphyte diversity in the Andes was highest between 1000 and 2000 m asl. They and Gentry (1988) also believed that epiphyte diversity increases with total rainfall and decreases with increasing length of dry season, suggesting drought as a limiting factor. The latter was based on the observations of the increase in berry fruited epiphytes and the decline in dust seeded orchids in the richest (wettest) sites. The present study however shows an exceptionally high diversity of wind dispersers. The climate within the study area is distinctly seasonal with a marked dry period, which suggests that other mechanisms other than moisture permanency may be influencing epiphyte species diversity at this site.

The Orchidaceae was by far the most important epiphyte family. Orchids are epiphyte specialists in all parts of the tropics and the results here are similar to most other neotropical epiphyte studies. In the present study, the diversity of the neotropical pleurothallid orchids is a feature, particularly the diversity in both *Pleurothallis* and *Stelis*.

In light of the small scale of the present study and the very high diversity of pleurothallid orchids, claims by Vásquez and Ibisch (2000) that the Bolivian Yungas are a centre of diversity for pleurothallid genera such as *Pleurothallis*, *Lepanthes* and *Trichosalpinx* are somewhat diminished. Such claims are based on the low number of vouchers from Peru, creating an apparent “speciation explosion in the Bolivian Yungas” (p. 458 Vásquez and Ibisch, 2000) due to the hole in Andean species distributions between Ecuador and Bolivia in the apparently depauperate Peru. Ibisch *et al*. (1996) also suggested that the percentage of epiphyte species in epiphyte rich genera in the Peruvian flora (particularly montane) was lower than had been estimated, that montane epiphytes were only a modest percentage of the montane flora, and that Peruvian epiphytes have low rates of endemism. Within both the latter works, there is little acknowledgement of the relative lack of plant collection in Peruvian montane forests caused by inaccessibility

and civil terrorism, and suppositions are based entirely on outdated Herbarium records (Brako and Zarucchi, 1993). In this study, based on Brako and Zarucchi (1993), a single tree would appear to hold 25% of Peruvian *Pleurothallis* (a genus of over 2000 species (Luer, 1986a)), 57% of Peruvian *Lepanthes* (a genus of over 600 species (Luer, 1996)) and 55% of Peruvian *Trichosalpinx* (a genus of 108 species (Luer, 1997)) to name a few. Clearly, the present study, being the first detailed epiphyte survey in the montane forests of Central Peru, highlights how far we are from identifying the Peruvian epiphyte flora. Developing hypotheses on the distributions and origins of epiphyte diversity within the Andes appears to be an unsound practice until the necessary collections are made to complete the incomplete Peruvian flora and balance the data from the region. Pleurothallids are likely to be equally diverse throughout the entire Andes once better collected.

3.5 Conclusion

The alpha diversity of the Ficus host is extraordinary and highlights the importance of the forest canopy for forest biodiversity. The study area lies within an ecoregion that is likely to have a very diverse epiphytic flora, despite lack of herbarium vouchers to demonstrate. The diversity of the Orchidaceae is particularly high, yet not surprising in the context of the total number of epiphyte species and individuals.

The explanation of such high species richness and abundance at a small spatial scale remains unclear and the unusual distribution of rare species in the community is likely to be an important factor. Evidence of epiphyte slumping, suggests a mechanism for the maintenance of a dynamic element within the epiphyte community. However, this mechanism appears to occur in many epiphyte communities with far lower species richness. Whatever the explanation, the three-dimensional distribution of the epiphyte community must be described in order to comprehend the mechanisms and processes that operate in the forest canopy.

Chapter 4 Habitat Characteristics and Distribution

4.1 Aims

This chapter describes the spatial distribution of epiphytes within the *Ficus* host in order to accomplish the second research aim.

2. Determine the distribution of the epiphyte flora within a single *Ficus* host tree in relation to habitat characteristics

Determining the spatial arrangement of epiphytes within the canopy is an important step in understanding the ecology of both the species and the community. It has been well established that, within the canopy, many epiphyte species have preferences in vertical canopy distribution (Bøgh, 1992; Freiberg, 1996; Hietz and Hietz-Seifert, 1995b; Ingram and Nadkarni, 1993; Johansson, 1978; Pupulin *et al.*, 1995; Rudolph *et al.*, 1998; ter Steege and Cornelissen, 1989). However, what environmental habitat factors determine these distributions is less well known. Geometric architectural factors such as branch angle and diameter (stability and space) have been investigated previously (Freiberg, 1996; Rudolph *et al.*, 1998) yet there has been little more than speculation about incident radiation. Some authors suggest that the complex canopy factors best summarised by the canopy zonation schemes (Gradstein *et al.*, 1996; Gradstein *et al.*, 2003; Nieder and Zotz, 1998) first conceived by Johansson (1974). Johansson (1978) later suggests that branch diameter is ideal for describing species distributions. Here, all the above methods are used.

Many factors were considered for the analysis. The research aim is achieved by 1). testing the relationships between the distribution of environmental habitat variables and epiphyte species and individuals, 2). analysing the distribution of epiphyte species and environmental habitat variables within Johansson Zones, and, 3). undertaking a multivariate analysis of the floristic composition of the epiphyte clumps and testing the relationships of the floristic variation to environmental variables.

4.2 Methods

In order to undertake the analysis of epiphyte distribution, 4% of the 632 clumps were removed from all analyses because of the lack of hemispherical image data (n = 606 clumps).

4.2.1 Environmental Habitat Variables

In order to understand the significance of relationships between epiphytes and environmental habitat variables, the relationships between the environmental habitat variables was scrutinised. This was achieved by creating a Pearson correlation matrix of all environmental habitat variables.

In order to context the variation of PAR and sky view variables within the canopy, the HemiView output from a hemispherical image taken above the Ficus crown was presented for comparison.

In order to describe the distribution of clump and environmental habitat variables throughout the canopy, the variables were plotted by branch diameters at 2 cm categories. Clump variables included clump abundance and clump richness.

4.2.2 Epiphyte Distribution by Environmental Habitat Variables

In order to describe the distribution of epiphyte individuals by each environmental habitat variable, clumps were first grouped into even and appropriately scaled categories. The sum of the abundances of all clumps within each scaled category was then plotted to show the distribution.

In order to describe the distribution of both epiphyte individuals and species by branch diameter only, clumps were grouped into the same even and appropriately scaled categories of branch diameter as used above. The sum of abundances of all clumps (again) and the number of different species within the scaled categories were grouped and plotted as above.

To describe the change in plant size with branch diameter, the most abundant species of the eight species for which data existed (Bromeliaceae sp. 2) was selected for display. Each of the four size classes were plotted by a

reduced scale of branch diameter classes due to the reduction in sample size.

In order to describe the distribution of epiphyte species by branch diameter, the abundances of species with a percentage frequency of ≥ 5% within the total number of clumps were summed and plotted to the same diameter categories used to describe plant size.

4.2.3 Epiphyte Distribution by Johansson Zones

In order to describe the community structure and composition, and, the distribution of epiphytes and environmental habitat variables within the *Ficus* host, all clumps were grouped by Johansson Zones.

In order to describe the community structure of each Johansson Zone, a dominance/diversity curve for each Johansson Zone were plotted to describe the distribution of species and were tested for goodness of fit to logarithmic models using SigmaPlot (SPSS Inc., 2001). The alpha diversity for each zone was also determined using the Fisher's-Alpha Index (α) (Fisher *et al.*, 1943), the Shannon Weaver Index (H') (Shannon and Weaver, 1949) and the Simpson's Index (D) (Simpson, 1949) (Equation 2). In order to determine species richness estimates of each zone, Jackknife species richness estimates and species area curves were produced for each zone using PC-ORD (McCune and Mefford, 1999).

In order to investigate the floristic composition of each Johansson Zone, a contingency table analysis using a Chi-Squared test was used to test for differences between zones in the expected abundance of species, lifeforms and taxonomic groups that showed a percentage frequency of ≥ 5% occurrence within the total number of upper canopy clumps. Species with ≤ 5% occurrence were grouped and included as 'other species'.

In order to investigate the habitat characteristics of the Johansson Zones, a 1-way ANOVA test was used to test for differences in environmental habitat variables between zones. Distributions of environmental habitat variables among zones were displayed with boxplots created in Minitab (2000).

In order to describe distribution among the Johansson Zones of the number of individuals, species and clumps, the scores were plotted by Johansson Zone. The means of clump and environmental habitat variables and the percentage abundance of within each zone of each common species, lifeforms and taxonomic group are described in order to facilitate discussion of the zone distributions. The percentage abundances were not used for the contingency table analysis.

In order to investigate the floristic similarity of Johansson Zones, an analysis of similarity test (ANOSIM) was performed on the zones using DECODA (Minchin, 2001). The dissimilarity matrix for ANOSIM tests was created with a Bray-Curtis dissimilarity coefficient and probabilities were calculated with 1000 random permutations.

4.2.4 Floristic Ordination

In order to investigate the relationship between all environmental habitat variables and the floristic composition, a floristic ordination was performed using Non-linear Multidimensional Scaling (NMS). The NMS ordinations were performed using PC-ORD (McCune and Mefford, 1999). The ordination technique used the method developed by Mather (1976) and Kruskal (1964) with a Bray-Curtis distance matrix. The ordination was run forty times from a random starting configuration with the real data and dimensionality was assessed with a Monte Carlo test with fifty runs of randomised data. DECODA (Minchin, 2001) was used for vector fitting of maximum correlation values of environmental habitat variables to the NMS ordination axis. The significance of the maximum correlation values was tested using 1000 permutations from a random starting configuration.

4.3 Results

4.3.1 Environmental Habitat Variables

The PAR and VisSky conditions at clumps display a high rate of radiation extinction by the canopy (Table 5). The highest pairwise Pearson correlation values between environmental variables were for TotBe – VisSky, TotBe – RadMidd, diameter – angle and diameter - LAIDev (Table 6). Generally, clump and environmental habitat variables showed a relatively large amount of variation at small branch diameters that was reduced with increasing diameter (Figure 16). The relationships of branch diameter to both branch angle and LAIDev were weakly positive.

Table 5: The VisSky (fraction) and PAR (mol. m^{-2} yr^{-1}) conditions found above the canopy (bold text) and the averages found at epiphyte clumps (italicised).

VisSky	TotBe	DirRadMidd	DirRadMorn	DirRadAft
0.60	**19922**	**1551**	**6320**	**1980**
0.09	*2747*	*717*	*233*	*289*

Table 6: The Pearson correlation matrix of environmental habitat variables including Johansson Zones.

	Ang	Dia	VisSky	TotBe	LAIDev	RadMorn	RadMidd
Dia	**0.578**						
prob	*0.000*						
VisSky	**-0.247**	**-0.152**					
prob	*0.000*	*0.000*					
TotBe	**-0.13**	**-0.074**	**0.836**				
prob	*0.001*	*0.069*	*0.000*				
LAIDev	**0.162**	**0.568**	**-0.117**	**-0.262**			
prob	*0.000*	*0.000*	*0.004*	*0.000*			
RadMorn	**0.037**	**0.296**	**0.232**	**0.397**	**0.128**		
prob	*0.369*	*0.000*	*0.000*	*0.000*	*0.002*		
RadMidd	**-0.061**	**-0.177**	**0.469**	**0.804**	**-0.411**	**0.142**	
prob	*0.131*	*0.000*	*0.000*	*0.000*	*0.000*	*0.000*	
RadAft	**-0.086**	**-0.078**	**0.423**	**0.353**	**-0.037**	**-0.337**	**0.075**
prob	*0.035*	*0.055*	*0.000*	*0.000*	*0.364*	*0.000*	*0.065*

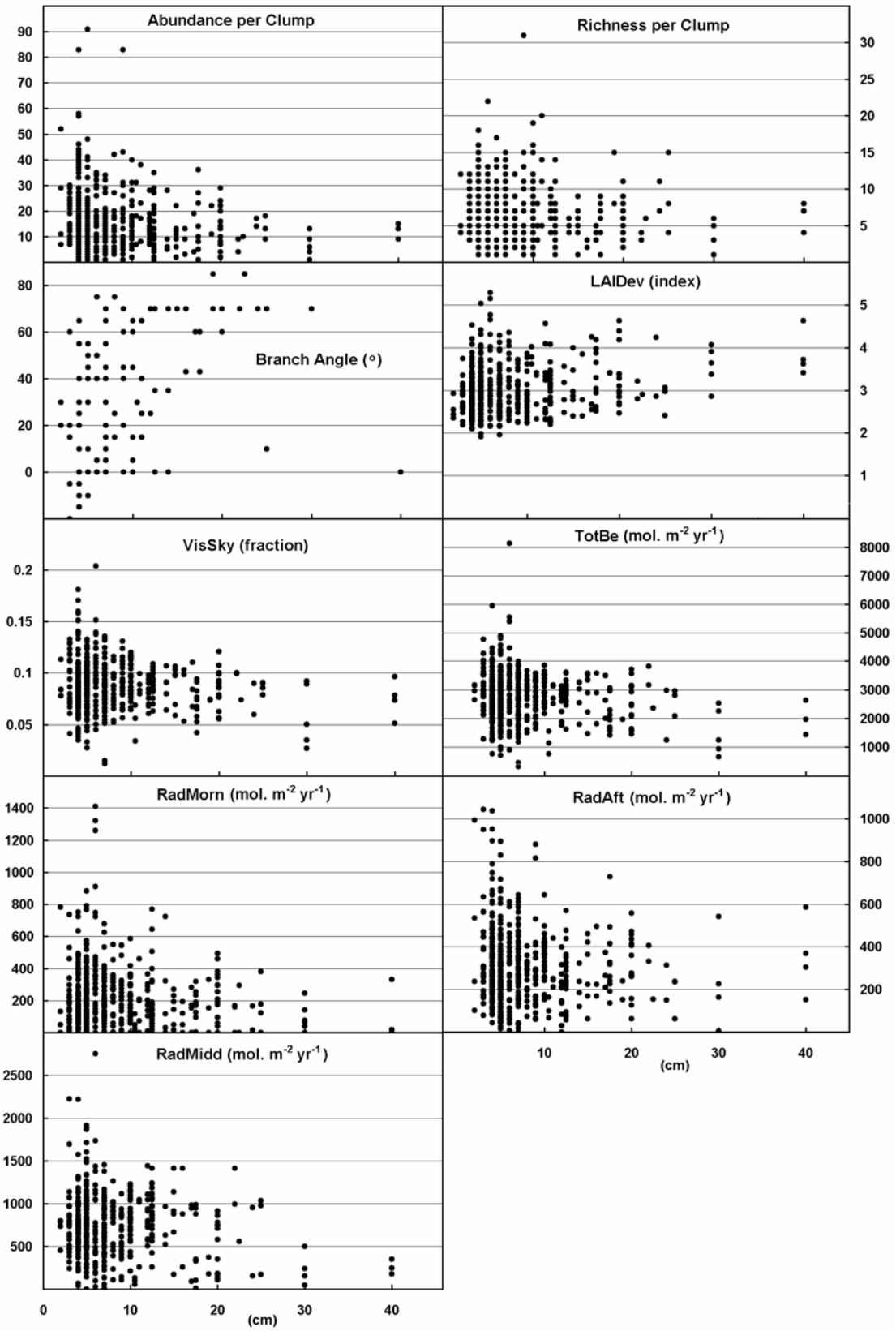


Figure 16: The branch diameter (X) versus all clump and environmental habitat variables.

4.3.2 Epiphyte Distribution

The strongest peak distribution of epiphyte individuals among all environmental variables was for branch diameter (Figure 17). The distribution of most common epiphyte species among branch diameters was similar to the trend for the number of individuals (Figure 20). Other species such as Bromeliceae sp. 2, *Elaphoglossum* sp. 7, *Maxillaria notylioglossa*, *Maxillaria* sp. 1 and *Prosthechea fusca* were most abundant on the smallest diameter branches.

Whilst epiphyte individuals were markedly concentrated on small branches, they showed no trend for branch angle. There were more epiphyte individuals present at lower values of LAIDev. The epiphyte abundance at VisSky and PAR values was normally distributed. The plant size distribution of Bromeliaceae sp. 2 did not show any variation with branch diameter (Figure 19). None of the other 8 species for which size data was collected showed any distribution trend for branch diameter. Species richness within the range of branch diameters was similar to the trend for the number of individuals (Figure 18). Ten epiphyte individuals were found on the underside of branches whilst humus accumulation was only observed on the topsides.

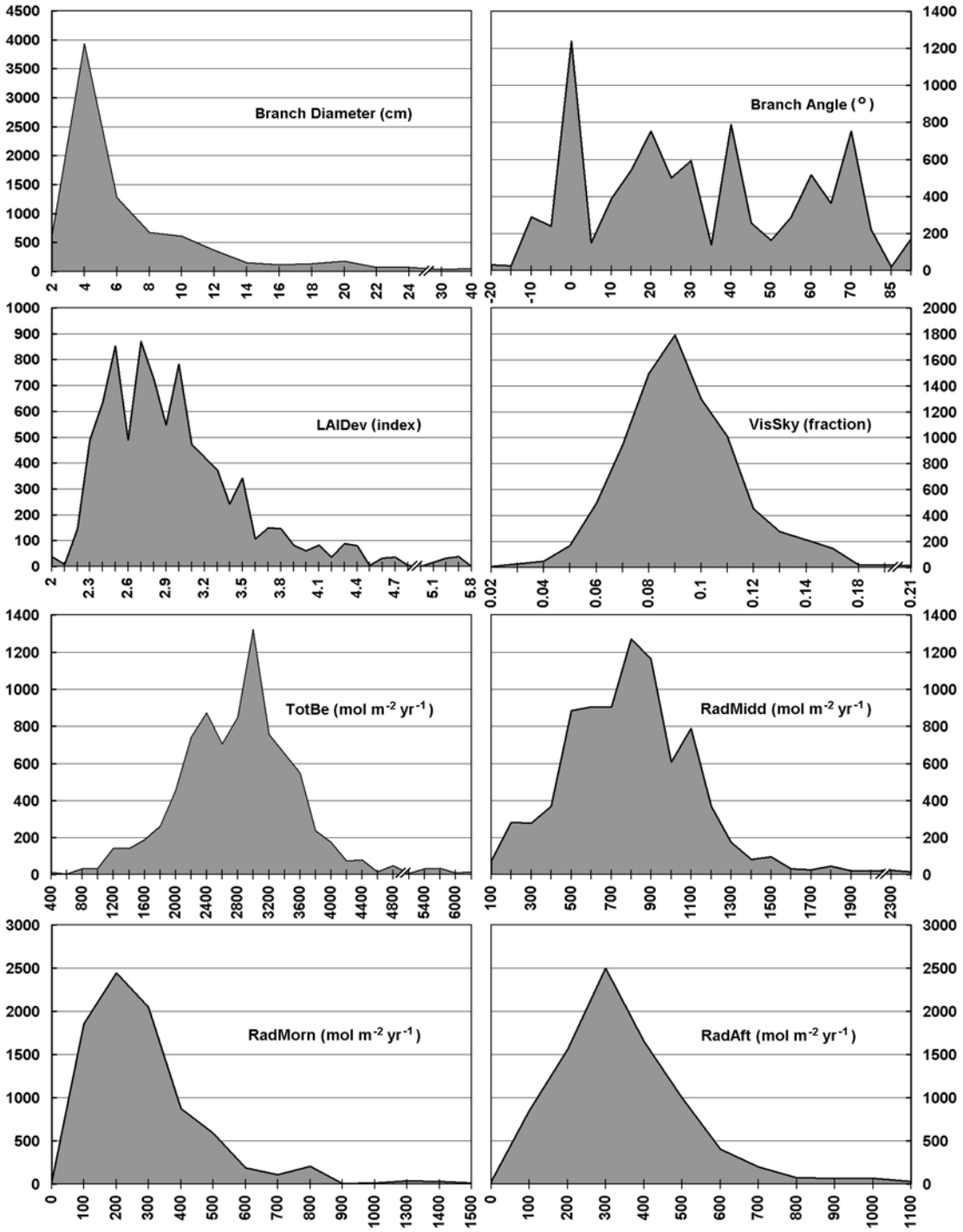


Figure 17: The distribution of epiphyte individuals (Y) found within the range of measured environmental habitat variable categories. Categories were creating by rounding up values to the nearest interval marked on each X axis. The branch diameter data presented excludes Zone 2.

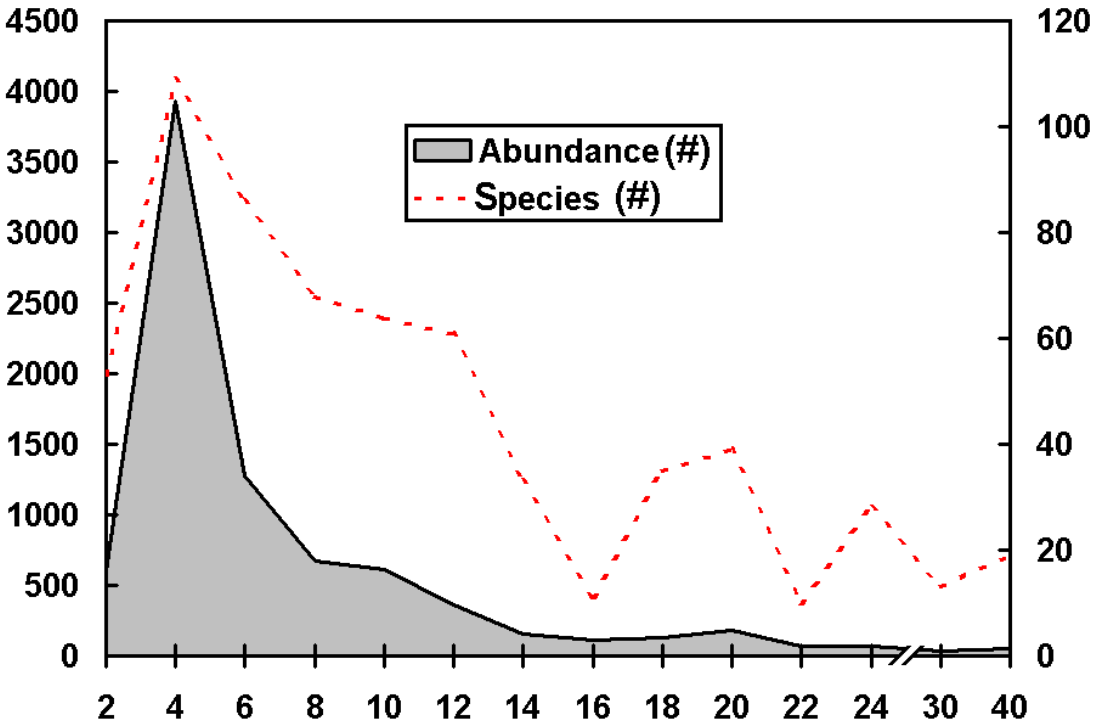


Figure 18: The distribution of epiphyte individuals (left axis) and species (right axis) within the range of branch diameters excluding Zone 2 data..

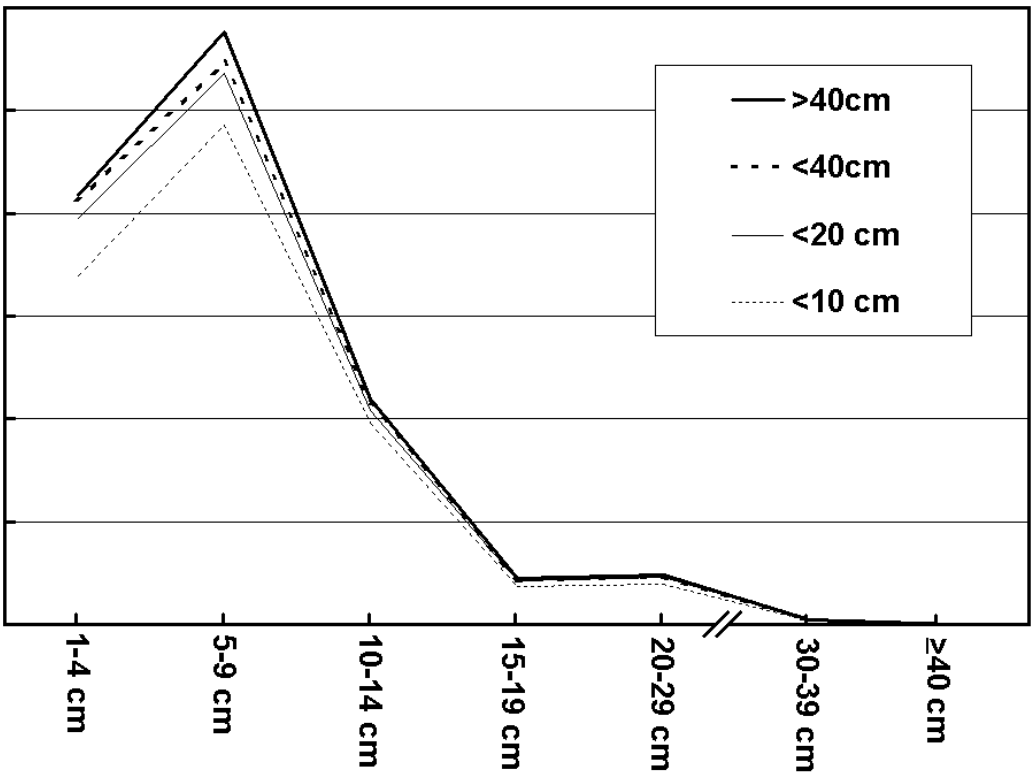


Figure 19: The abundance trends (Y) of 4 size classes of Bromeliaceae sp. 2 at 5 cm branch diameter categories (X).

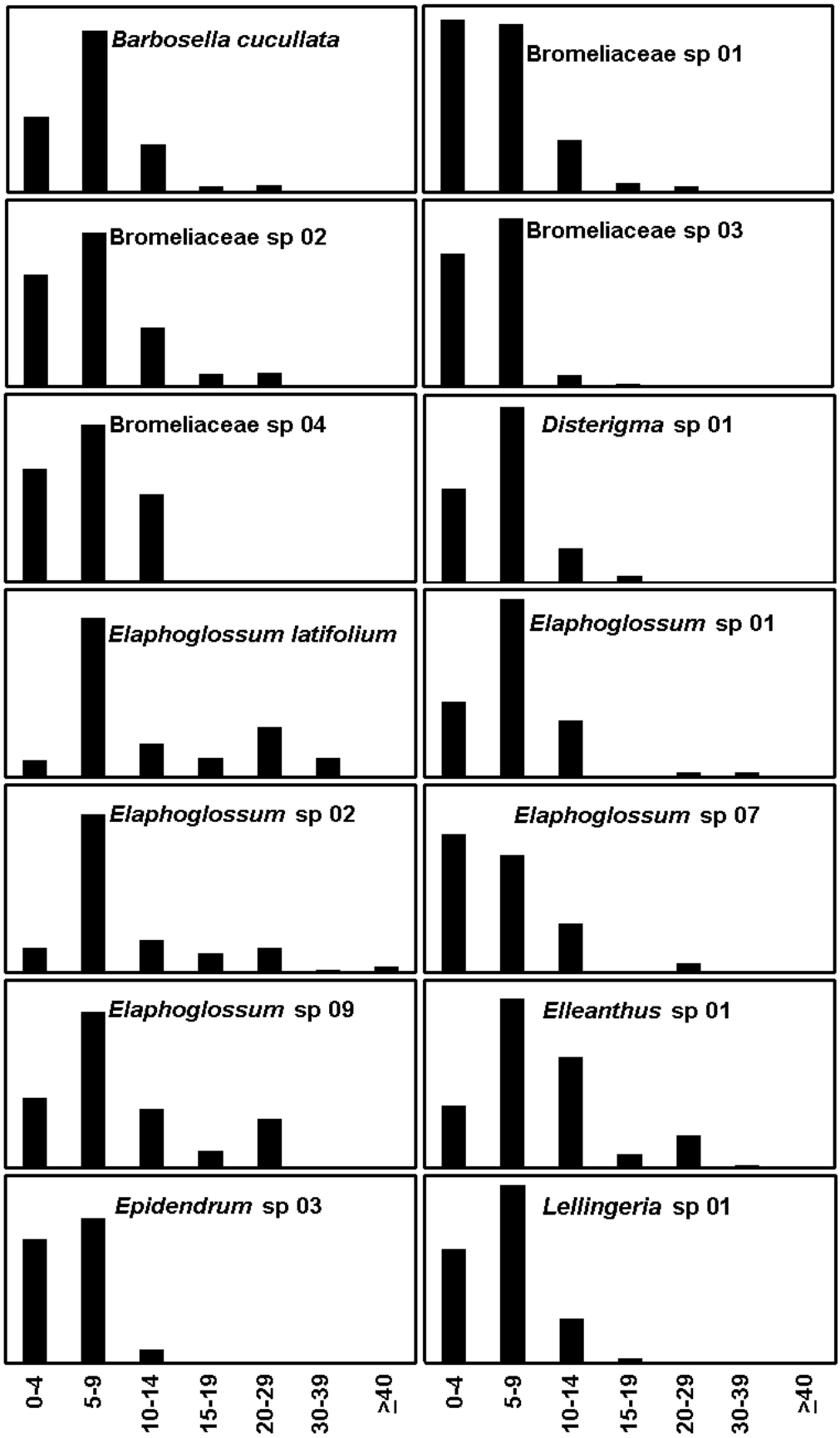


Figure 20: A. The distribution of common species among branch diameters (cm).

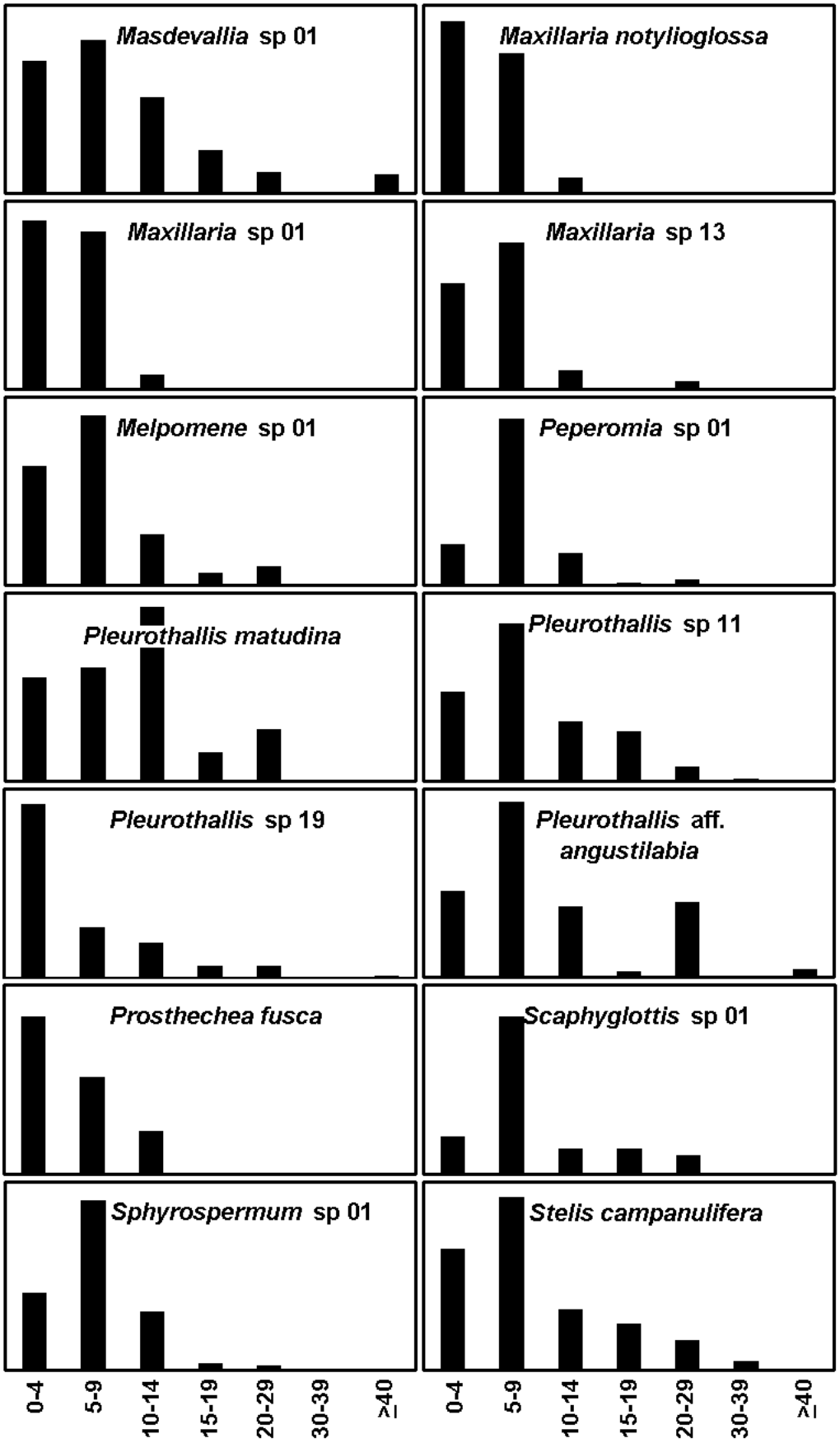


Figure 20: B. The distribution of common species among branch diameters (cm).

4.3.3 Johansson Zones

4.3.3.1 Community Structure

The dominance/diversity curves within each zone displayed lognormal distribution (Figure 21). However, the distortion in the Zone 3 curve appeared to suggest the presence of a second guild of species. Again, rare species proportions are high. The species area curves for Zone 2 and 3 remained steep, whereas Zone 4 and 5 showed signs of slight levelling (Figure 22). Zone 5 had the highest amount of individuals and clumps and Zone 4 had the highest species richness (Figure 23). Jackknife species richness estimates for each zone were considerably larger than the richness found and the alpha diversity indices ranked the zones in two directions (Table 7). The Jackknife estimates for Zone 5 were higher than Zone 4. The α ranked Zone 5 the highest and Zone 3 the lowest. The H' and D ranked Zone 5 the lowest and Zone 3 the highest. Generally, the index values of all zones were within a relatively close range to the values for the whole tree (Section 3.3.2).

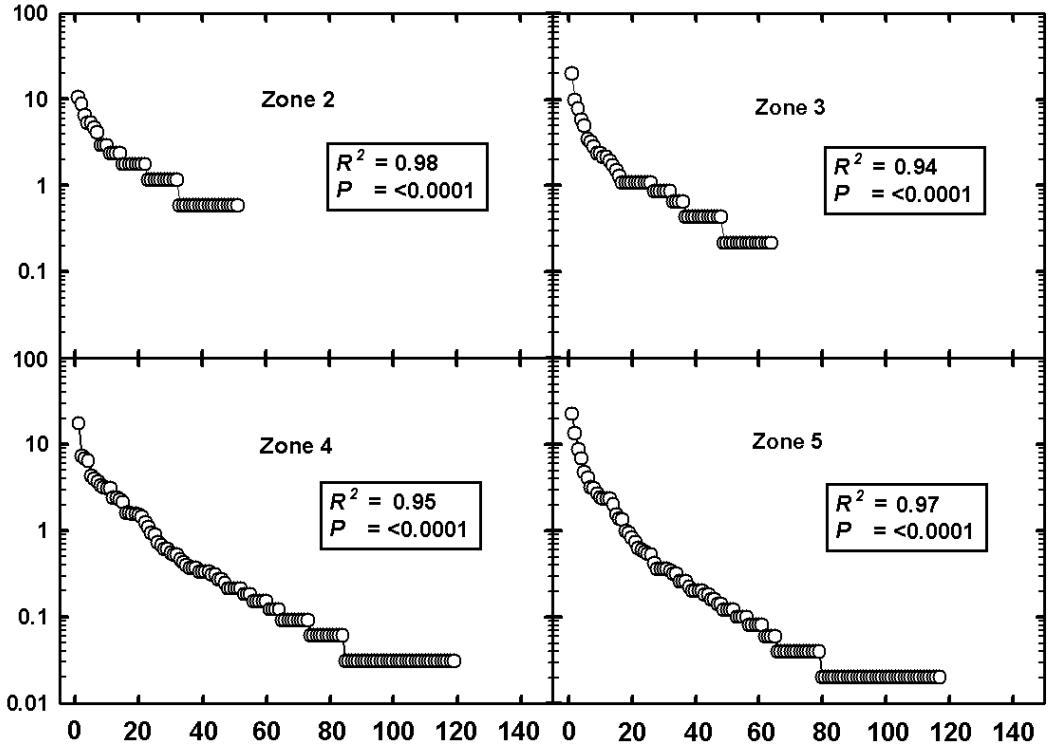


Figure 21: Dominance/diversity curves for Johansson Zones. Percentage abundance on a log scale (Y) of all epiphyte species in rank order of abundance (X).

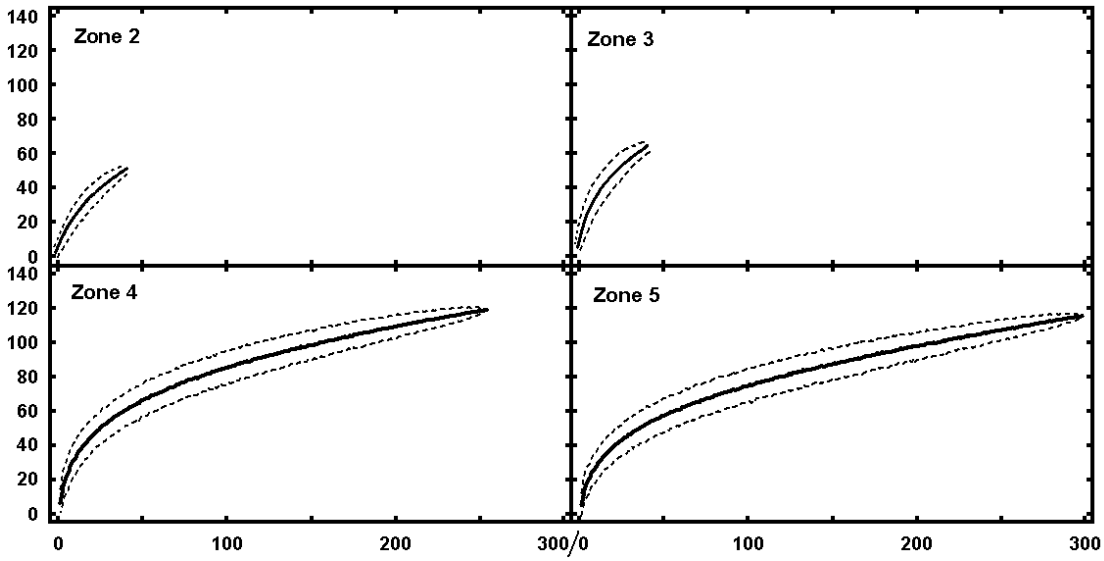


Figure 22: Species Area Curves for Johansson Zones calculated using a Sørenson distance matrix. Average accumulation of species (Y) is plotted against the number of clumps (X). Dotted lines represent ± 1 standard deviation

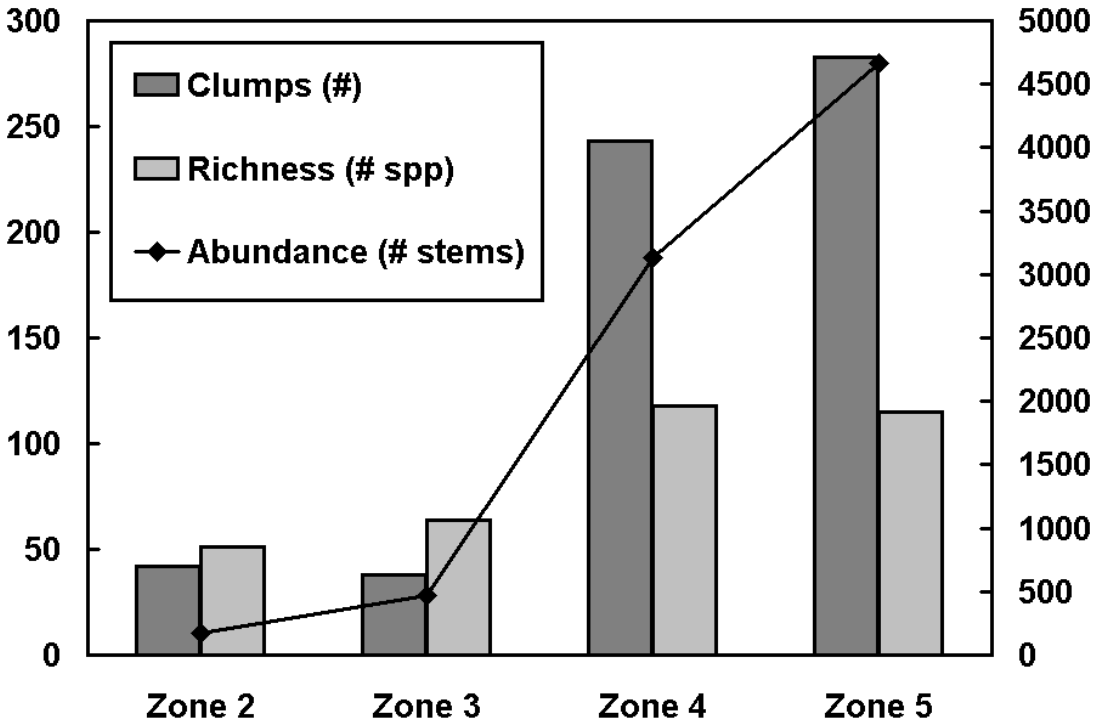


Figure 23: The number of epiphyte clumps, the species richness and the abundance of epiphytes (right axis) in each Johansson Zone

Table 7: Individuals, species richness, jackknife estimates of species richness and diversity index scores for all Johansson Zones

	Zone 2	Zone 3	Zone 4	Zone 5
Individuals	172	465	3134	4662
Species Richness	51	64	118	115
First-order Jackknife Estimate	76.4	90.3	161.8	165.8
Second-order Jackknife Estimate	91.9	107.6	191.6	202.6
Fisher's Alpha	17.77	9.79	64.22	69.55
Shannon's Index	3.53	3.35	3.48	3.07
Simpson's Index	0.96	0.93	0.94	0.91
Species with 1 Occurrence	26	27	43	49
Species with 2 Occurrences	10	9	13	12

A total of 52% of all species were found only in one zone. However, many of these were single or double occurrence species. Zone specificity was found in 31% of Zone 2 species, 17% of Zone 3 species, 27% of Zone 4 species and 32% of Zone 5 species. The Percentage Abundance (PA) of common species, lifeform and taxonomic groups were generally lowest in Zone 2 and 3 (Table 8). In Zone 2, 13% of common species had their highest PA. In Zone 3, 7% of common species had their highest PA. In Zone 4, 34% of common species had their highest PA and in Zone 5, 37% of common species had their highest PA.

4.3.3.2 Clump and Environmental Habitat Variables

All clump and environmental habitat variables have an uneven distribution across Johansson Zones (Figure 24). There were significant differences between Johansson Zones for all clump and environmental habitat variables (1-way ANOVA) (Table 8). Average branch angles and branch diameters decreased from Zone 2 to Zone 5. Zone 2 had lower abundance per clump and lower richness per clump. LAIDev decreased from Zone 2 to Zone 5. VisSky mean values were equal in Zone 4 and 5, and also in Zone 2 and 3. TotBe values were markedly lower in Zone 3. RadMidd was lowest in Zone 3 and highest in Zone 5. RadMorn was significantly higher in Zone 2 and RadAft was lowest in Zone 3.

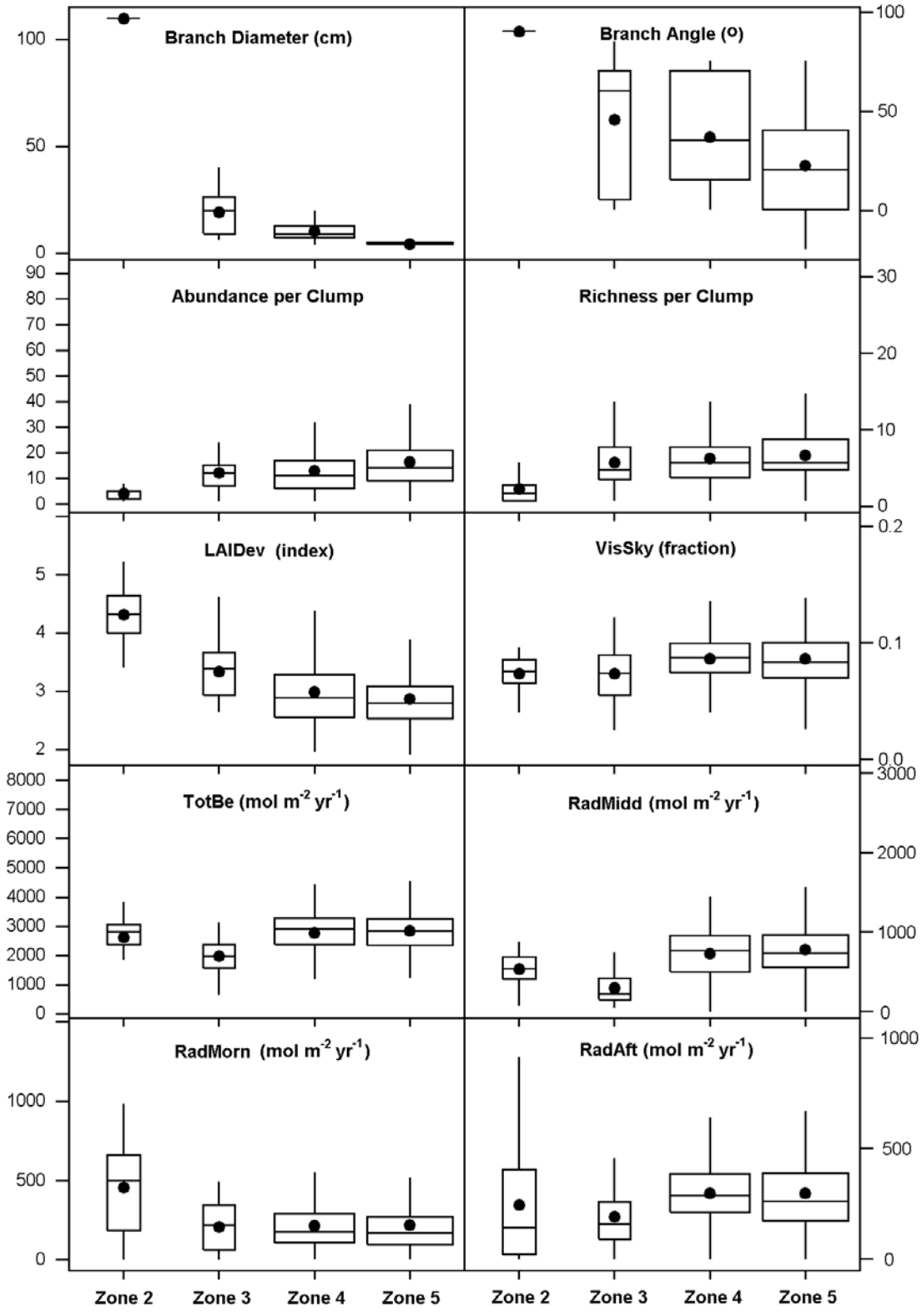


Figure 24: Boxplots of clump and environmental variables within Johansson Zones. Boxes represent the 2nd and 3rd quartile separated by the line at the median. Whiskers extend to the lower limits of the 1st quartile and the upper limits of the 4th quartile. Closed circles represent the mean and box width is relative to sample size.

Table 8: The clump and environmental variable means and the percentage abundance of lifeforms, taxonomic classes and common species within Johansson Zones.

Johansson Zone	Zone 2	Zone 3	Zone 4	Zone 5	
Abundance (#)	**172**	**465**	**3134**	**4662**	
Clumps (#)	**42**	**38**	**243**	**283**	
Abundance/Clump (#)	4.1	12.2	12.9	16.5	***
Richness/Clump (#)	2.6	6.0	6.5	7	***
Branch Diameter (cm)	106.4	19	10.5	4.4	***
Branch Angle	90	45.3	36.7	22.2	***
LAIDev (index)	4.3	3.3	3	2.9	***
VisSky (fraction)	0.075	0.075	0.088	0.088	***
TotBe (mol.m2/year)	2629	1968	2773	2848	***
RadMidd (mol.m2/year)	537	301	736	785	***
RadMorn (mol.m2/year)	457	209	214	220	***
RadAft (mol.m2/year)	246	193	301	300	**
Ascending	**6.4**	**6.5**	**6.3**	**4**	***
Caespitose	**28.5**	**33.3**	**21.7**	**16.5**	***
Lepanthid	**4.1**	**2.4**	**1.9**	**0.8**	***
Long Creeping	**14.5**	**9**	**7.7**	**1**	***
Long Repent	**6.4**	**2.4**	**12.7**	**33.3**	***
Open Tank	**0.6**	**21.3**	**27.1**	**25.7**	***
Pendant	**12.8**	**2.8**	**1.1**	**0.6**	***
Short Creeping	**7.6**	**3.2**	**9.7**	**10**	***
Short Repent	**8.1**	**14.2**	**11.2**	**7.5**	***
Bromeliad	**0.6**	**21.3**	**27.6**	**26**	***
Herb	**6.4**	**1.3**	**1.9**	**0.9**	***
Orchid	**3.5**	**11.2**	**17.3**	**37.6**	***
Pleurothallid	**41.9**	**44.3**	**29.1**	**21.3**	***
Fern	**34.9**	**17.4**	**17.7**	**9.9**	***
Woody Dicot	**6.4**	**3.7**	**6.4**	**4.1**	***
Barbosella cucullata	**0.6**	**1.1**	**3.4**	**2.4**	**
Bromeliaceae sp 01	**0**	**1.1**	**7.1**	**6.8**	***
Bromeliaceae sp 02	**0**	**19.8**	**18**	**14**	***
Bromeliaceae sp 03	**0**	**0**	**0.7**	**3.1**	***
Bromeliaceae sp 04	**0**	**0.4**	**0.8**	**0.7**	**NS**
***Disterigma* sp 01**	**0**	**0.2**	**1.3**	**1.2**	**NS**
Elaphoglossum latifolium	**0**	**4.9**	**3**	**0.2**	***
***Elaphoglossum* sp 01**	**0**	**0.2**	**1.1**	**0.7**	*
***Elaphoglossum* sp 02**	**1.7**	**1.9**	**2.5**	**0.4**	***
***Elaphoglossum* sp 07**	**1.2**	**1.7**	**4.1**	**4.3**	*
***Elaphoglossum* sp 09**	**0**	**1.1**	**1.3**	**0.4**	***
***Elleanthus* sp 01**	**0.6**	**2.8**	**3**	**0.9**	***
***Epidendrum* sp 03**	**0**	**0.2**	**1.3**	**2.3**	***
***Lellingeria* sp 01**	**0.6**	**0.2**	**2.2**	**2.4**	**
***Masdevallia* sp 01**	**0.6**	**5.8**	**3.2**	**2.5**	**
Maxillaria notylioglossa	**0**	**0**	**6.3**	**22**	***
***Maxillaria* sp 01**	**0**	**0**	**1.6**	**8.7**	***
***Maxillaria* sp 13**	**0**	**0**	**0.4**	**1.3**	***
***Melpomene* sp 01**	**0**	**0.4**	**1**	**0.6**	**NS**
***Peperomia* sp 01**	**1.2**	**0.4**	**1.6**	**0.9**	*
Pleurothallis* aff. *angustilabia	**2.3**	**7.7**	**1.6**	**1.5**	***
Pleurothallis matudina	**0.6**	**1.5**	**2.4**	**0.4**	***
***Pleurothallis* sp 11**	**0**	**3.4**	**4.4**	**2.6**	***
***Pleurothallis* sp 19**	**1.2**	**3.2**	**2.2**	**3.4**	*
Prosthechea fusca	**0**	**0**	**0.6**	**0.8**	**NS**
***Scaphyglottis* sp 01**	**0**	**0.9**	**0.7**	**0.4**	**NS**
***Sphyrospermum* sp 01**	**1.2**	**1.1**	**3.5**	**1.9**	***
Stelis campanulifera	**1.2**	**9.7**	**6.4**	**4.7**	***
Other spp.	**87.2**	**30.1**	**14.2**	**8.5**	***

Clump/Environmental Variables: 1 - way ANOVA
Community Variables: Chi-Squared test

NS : no significant differences
*** : P < 0.05**
**** : P < 0.001**
***** : P < 0.0001**

4.3.3.3 Floristics

There were significant differences in the PA and expected PA across Johansson Zones of all lifeforms and taxonomic classes, and most epiphyte taxa (Chi-Squared test) (Table 8). All common lifeform groups were represented in all zones. Ascending plants have a low PA in Zone 5. The caespitose lifeform has the highest PA of Zone 2 and 3, and is the second and third highest in Zones 4 and 5 respectively. The PA of the lepanthid lifeform, the long creeping lifeform and pendant lifeform decrease from Zone 2 to 5. The long repent lifeform has the highest PA in Zone 5. The open tank lifeform has high PAs in all zones except for Zone 2 where it has the lowest PA of all lifeforms. The short creeping lifeform has lowest PA in Zone 3, whereas the short repent lifeform has the highest PA in Zone 3.

All common taxonomic groups were represented in all zones. The bromeliads have high PAs in all zones except for Zone 2 where they have the lowest PA of all groups. The herbs had their highest PA in Zone 2. The orchids decreased in PA from Zone 5 where they had the highest PA of all groups. The pleurothallid orchids were an important group in all zones and have the highest PA in Zone 2, 3 and 4. The ferns decreased in PA from Zone 2. The woody dicots had a low PA in all zones but were lowest in Zone 3.

Eighty-two percent of common species had significantly different PA in some zones. Fifty-seven percent of common species were not represented in Zone 2, 14% were not represented in Zone 2 and 3, and all common species were represented in Zone 4 and 5. The proportion of ‘other species’ decreased considerably from Zone 2. In Zone 2, no common species had their highest PA and the highest PA was the ‘other species’. In Zone 3, 17% of common species had their highest PA and the highest PA was from the ‘other species’ followed by Bromeliaceae sp. 2. In Zone 4, 35% of common species had their highest PA and the highest PA was Bromeliaceae sp. 2 followed by the ‘other species’. In Zone 5, 28% of common species had their highest PA and the highest PA was *Maxillaria notylioglossa* followed by Bromeliaceae sp. 2.

The ANOSIM test performed on Johansson Zones described the

overlap of floristic communities in adjacent zones. While all zones had significantly different floristic compositions, adjacent zones were more similar than those further apart, and the most dissimilar adjacent zones were Zone 2 and 3 (Table 9). The similarity between Zone 3 and 4 was the highest, whereas the dissimilarity between Zone 2 and 5 was the highest.

Table 9: ANOSIM results for Johansson Zones. R = 0.323, *P* = 0.0000

	Zone 2	*prob*	**Zone 3**	*prob*	**Zone 4**	*prob*
Zone 3	0.2818	*0.000*				
Zone 4	0.6140	*0.000*	0.0917	*0.017*		
Zone 5	0.8553	*0.000*	0.5200	*0.000*	0.1834	*0.000*

4.3.4 Floristic Ordination

The NMS ordination resulted in a three dimensional solution with a moderately high minimum stress (stress = 24.634%). Further dimensions reduced stress but were within the range obtained with randomised data by the Monte Carlo test. The highest vectors of maximum correlation were those of Johansson Zone and branch diameter (Table 10). The maximum correlation of LAIDev was also strong. Zone 2 was well defined in ordination plots on axes 1 and 3 while Zone 4 and 5 were best differentiated on Axes 1 and 2 (Figure 25). Large branch diameters were well defined on axes 1 and 3 while smaller diameters were best defined on axes 1 and 2 (Figure 26). The ordination plots show a large amount of overlay between Zone 4 and 5 clumps.

Table 10: Vectors of maximum correlation for environmental habitat variables for NMS of all clumps.

Variable	**max R**	prob
Zone	0.65	0.000
Angle	0.36	0.000
Diameter	0.61	0.000
LAIDev	0.49	0.000
VisSky	0.17	0.000
TotBe	0.20	0.000
DirRadMidd	0.28	0.000
DirRadMorn	0.17	0.002
DirRadAft	0.07	NS

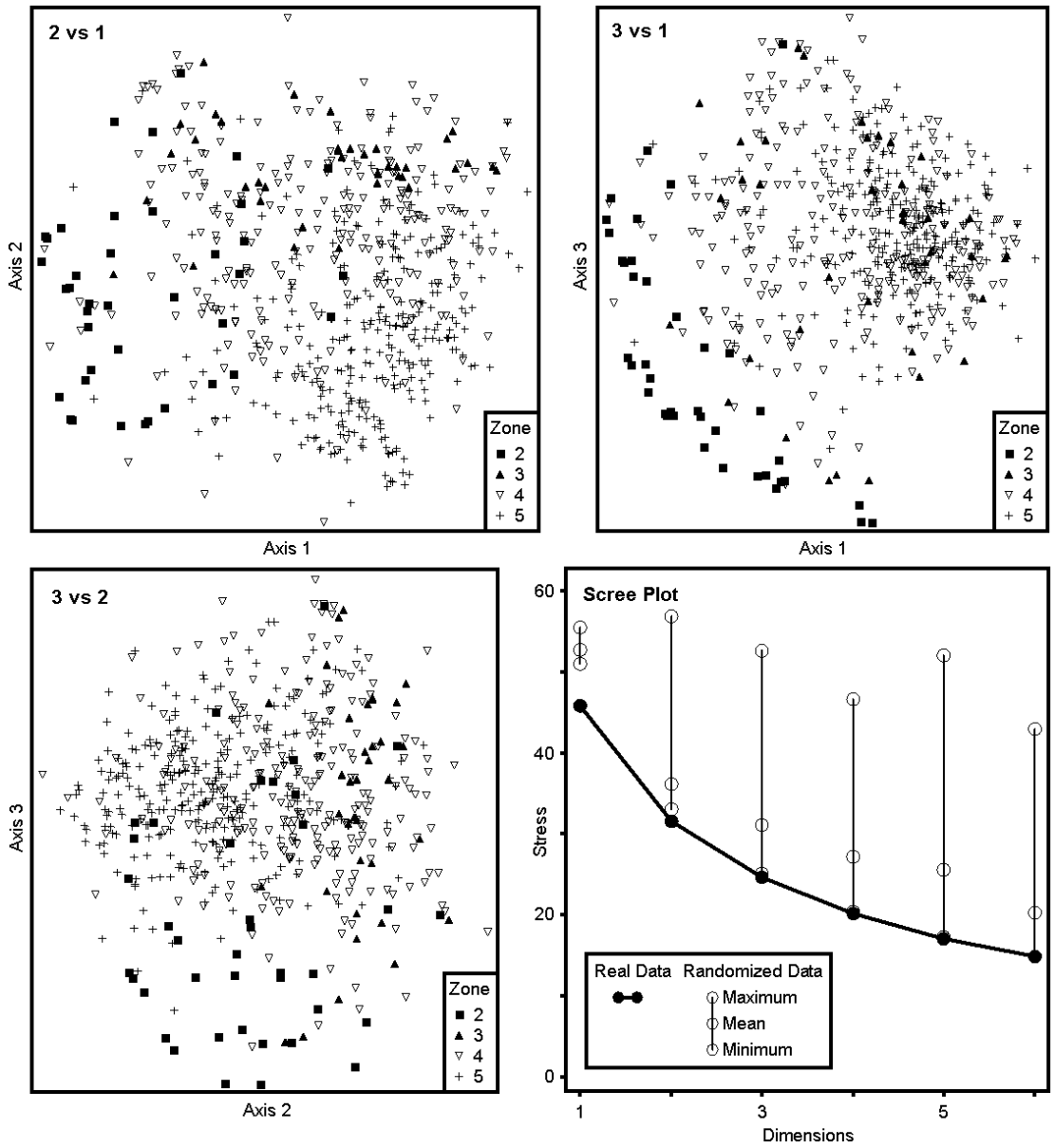


Figure 25: Non-Linear Multidimensional Scaling ordination plots of all clumps classified by Johansson Zone and the Scree plot indicating stress levels at each dimension.

4.4 Discussion

4.4.1 Environmental Habitat Variables

Judging by the range of all radiation values throughout the whole tree relative to above the canopy values provided, the leaf edge surface of the *Ficus* host appears efficient in providing ample shaded habitat for canopy epiphytes. However, when plotted by branch diameter, the lower PAR values

of TotBe, RadMorn, RadMidd and RadAft show a distribution across all branch diameters. Despite the high variation in all PAR and VisSky values of smaller diameters of the outer canopy, the plotted data does shows that radiation was generally lower on larger diameters towards the inner canopy. The higher variation in radiation receipt at the smaller diameters than the large ones can be explained by the closer proximity to the canopy leaf surface. This offers stochastically distributed low PAR opportunities directly below dense leaves/branches as well as high PAR opportunities in gaps.

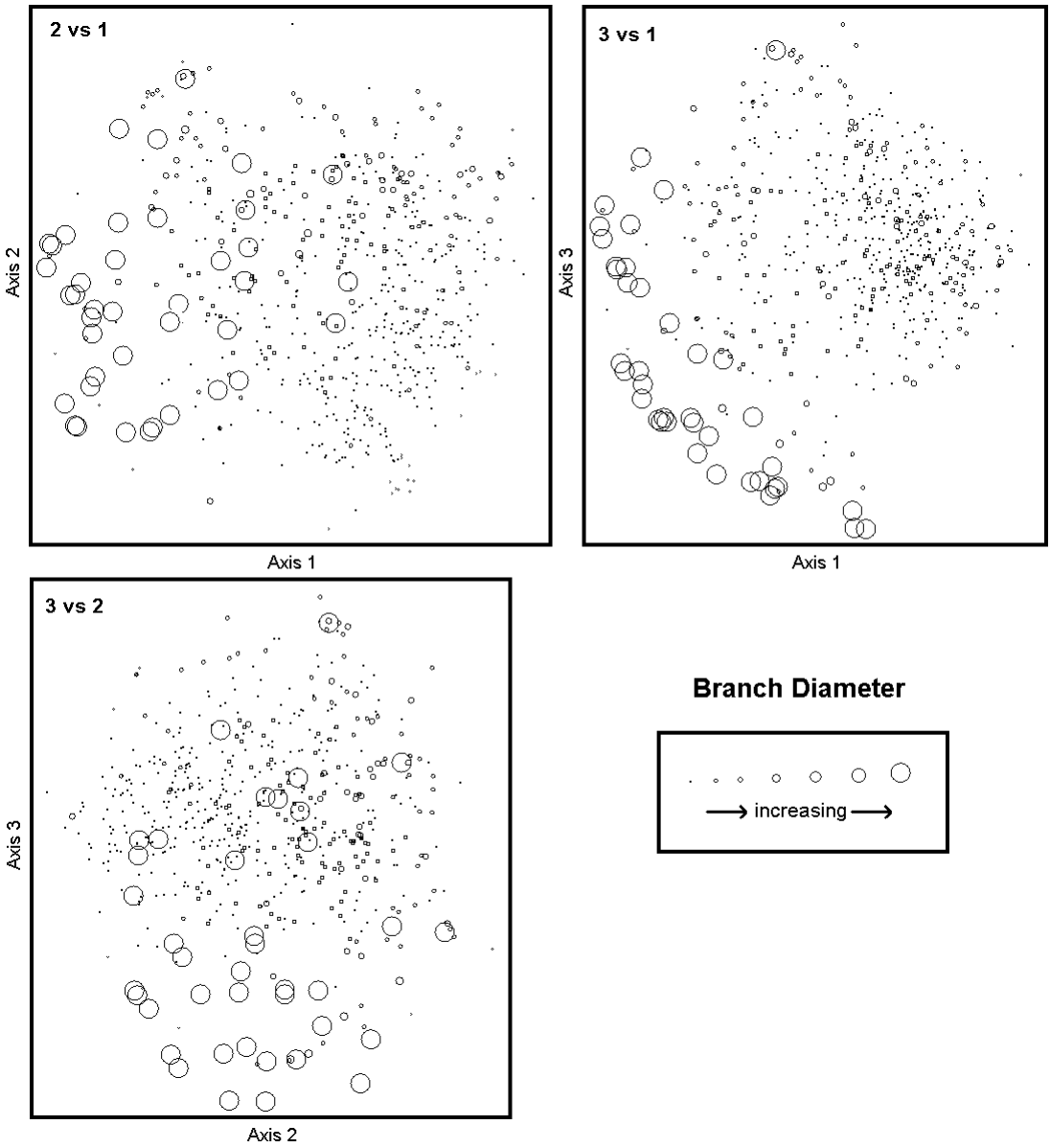


Figure 26: Non-Linear Multidimensional Scaling ordination plots of all clumps classified by branch diameter.

It was not surprising that some of the variables generated from the hemispherical images were highly correlated. TotBe is calculated from two aspects of the hemispherical images. The diffuse portion is related to the sky obstructions of the entire sky (VisSky value) and the direct portion comes from the sky obstructions of the sun's path. Despite the variance between the two factors that might be expected throughout the canopy, the correlation indicates that many areas of the canopy (predominantly from Zone 4 and 5) are structurally similar. The high correlation of TotBe with DirMidd (0.8), indicates that variation in morning and/or afternoon radiation receipt has little effect on total radiation over the range of clumps.

Branch diameter was related to other structural variables. Rudolph *et al.* (1998), found a negative relationship (not shown statistically) between branch angle and branch diameter, though the study was of selected branches and did may not have encompassed the variation within tree crowns. This is expected in phorophytes with a vertically inclined architecture where the canopy surface lies above the branching nodes. In the present study the relationship was moderately positive, as being a large forest emergent, major branching systems took all angles including negative ones (Figure 27). Likewise, the emergent structure also appears to explain the lack of relationship between branch diameter and TotBe or any of the radiation variables. The distribution of TotBe appeared to evenly distributed given the lower frequency of values at larger diameters.

4.4.2 Epiphyte Distribution

The concentration of epiphyte individuals on small diameter branches in tropical forest has only been reported previously by Pupulin *et al.* (1995) at 1600 m asl in Costa Rica (only orchids described), by Rudolph *et al.* (1998) at 1700 m asl in Ecuador, and by Catling *et al.* (1986) in a Belizean grapefruit orchard. The presence of the highest epiphyte richness on smaller diameter branches has been only reported previously by Pupulin *et al.* (1995). However, given that they did not report on any other epiphytes than orchids, the present study is the first to report a greater diversity of epiphyte species in an entire community on smaller diameter branches. This is not likely to be a

rare phenomenon, but a reflection of both the dearth of montane epiphyte studies and the variation in crown architecture between the *Ficus* host of the present study and the few others studied to date. Furthermore, the distribution should not be surprising given that the epicenter of diversity for obligate twig epiphytes is the neotropics (Chase, 1987) and that significant areas of the neotropics remain unstudied. The above-mentioned pattern extended to the distribution of all common species. Of these, some displayed the extreme of the pattern with their highest abundance in the smallest diameter class indicating a coloniser status.

The pattern of thickening of the outer canopy by epiphytes and arboreal humus was easily recognized during the sampling, though what was more surprising was the absence of epiphyte clumps on larger branches, assumedly due to the phenomenon of epiphyte slumping (Section 3.4.3). The pattern could not be explained by the coalescence of clumps with age, as the number of individuals of inner canopy clumps was relatively low. Freiberg (1996) also reported the assumed influence of slumping within the inner canopy branches of his study.

Large branches of the inner canopy were characterized by high branch angles that would exacerbate any slumping mechanism in a smooth-barked host. Following the pattern of lower epiphyte abundance in the inner canopy, species richness also showed a decline. This does not represent an equilibrium through competition and dominance, but highlights the non-equilibrium of the community though epiphyte slumping. Thus, with increasing branch diameter from those that represent the peak in epiphyte abundance and diversity, the diversity of successional stages also increases. This was also found in emergent hosts by Freiberg (1996).

Hietz (1997), Rudolph *et al.* (1998) and Freiberg (1999) described a reduction in plant size and an increase in juveniles with decreasing branch diameter. This explained the high epiphyte abundance on smaller diameter branches found by Rudolph *et al.* (1998). In the present study, the most common bromeliad species showed no sign of any plant size-diameter trend and nor did any of the other eight species for which data was collected (data

not shown for 8 other species). This contrast with the relationships for bromeliads found by Hietz (1997). Furthermore, very small orchid juveniles contributing to the distribution pattern found by Rudolph *et al.* (1998) were not collected in the present study. Thus, in the present study, the pattern of high epiphyte diversity and abundance in the outer parts of the canopy are different to the most comparable study.

The lack of trend in the distribution of epiphyte individuals by branch angle relates to the emergent structure of the tree. Similar results were found in emergent trees by Freiberg (1996). While branch diameter was influential for epiphyte abundance, branch angle had no clear effect throughout the tree. This suggests that relationships found between branch angle and the distribution of some epiphytes in typical canopy trees with little structural diversity may be artefacts of other factors. Despite the strong relationship between diameter and angle, Rudolph *et al.* (1998) did not attribute their large number of epiphytes on small diameter branches to be related to branch angle. They did however report the negative relationship of branch angle and substrate thickness (accumulated humus layer).

Branch angles may partly explain the abundance of epiphytes on small branch diameters. Branch angle negatively affects the accumulation of humus (Ingram and Nadkarni, 1993; Nadkarni and Matelson, 1991; Rudolph *et al.*, 1998), necessary for the establishment and survival of many vascular epiphytes (Dudgeon, 1923; Freiberg, 1996; Johansson, 1974). In many phorophytes of closed canopies, outer canopy twigs are also associated with higher branch angles (Rudolph *et al.*, 1998) that reduce humus accumulation. Thus, in the present study, because of the heterogeneous canopy, the phorophyte branching architecture and the emergent stature, the abundance of low branch angles within the outer canopy may increase the humus retention capacity relative to what is commonly found. This increases the likelihood of humus dependent species occurring on the smaller branch diameters alongside obligate twig epiphytes.

An explanation for the increased diversity of epiphytes on smaller diameters lies partly in the explanation above, but could also be the result of

the demonstrated diversity of PAR conditions at small branch diameters. An increased diversity of PAR distribution could allow species with diverse PAR requirements/tolerances to coexist in the outer canopy. However, in Monte Verde Costa Rica, artificially created branch-fall gaps, that apparently change exposure regimes in upper canopies, appeared to have little effect on epiphyte community composition (Rosenberger and Williams, 1999). However, the study did not measure PAR receipt or the changes to radiation receipt at high zenith angles, and the one-year sampling period may not have been sufficient to detect composition changes in long-lived communities.

4.4.3 Johansson Zones

4.4.3.1 Community Structure

The dominance/diversity curves within each zone follow the same lognormal trends seen for the entire community. This may suggest that it is unlikely that the floristic composition of any zone is more or less developed than any others. The distortion in the curve observed for Zone 3, suggests the presence of a second guild of species that would be expected to be better represented by a broken-stick model. The lack of fit to other models over the general lognormal model is a common trend due to the flexibility and ease of fit from the highly parameterised lognormal model (Wilson, 1993). The two guilds in Zone 3 are likely to represent the two distinct niches of Zone 3, the large and deep humus deposit at the top of the trunk from which arise the principal branches, and the surface of the wide and high angle principal branches. This suggests that the Johansson scheme might require a revision if each zone is to adequately summarise an individual habitat zone.

The species area curves show that the tree does not represent all species likely to occur in Zone 2 and 3 on all *Ficus* throughout the forest. Likewise, the jackknife estimations of Zone 2 and 3 species richness are considerably higher than those observed. This was expected given the small sample size obtainable relative to the upper canopy, and the sparse patterns of trunk epiphyte species distributions (Catling and Lefkovitch, 1989; Moran *et al.*, 2003; Tewari *et al.*, 1985).

Species area curves for the upper zones displayed a higher degree of levelling relative to Zone 2 and 3. However, they too indicate that total species richness in Zone 4 and 5 on *Ficus* throughout the forest should be higher than the observed. Though H' and D was lower in Zone 5, jackknife estimators predicted a higher species richness than the more diverse and rich Zone 4. This suggests that Zone 5 has a larger proportion of sparsely distributed species.

Similar to epiphyte distribution among branch diameters, the distribution of epiphyte individuals and clumps was concentrated in Zone 5. This pattern of distribution is the opposite of most epiphyte distributions previously reported. van Leerdam *et al.* (1990) in Columbia, Ingram and Nadkarni (1993) in Costa Rica, Freiberg and Freiberg (2000), Rudolph *et al.* (1998) and Bøgh (1992) in Ecuador, ter Steege and Cornelissen (1989) in British Guyana, Freiberg (1996) in French Guiana, Kelly (1985) in Jamaica, Nauray Huari (2000) in Peru, and Johansson (1978) in West Africa, all found that in montane and/or lowland forests, epiphyte density/cover was higher towards the centre of the tree crowns. This results from lower desiccation rates in the inner crown in such forests (Freiberg, 1996; Johansson, 1974). In the present study, these distribution patterns are reversed, though Zone 3 clumps still have the lowest VisSky and PAR values, indicating the highest shading by the canopy.

4.4.3.2 Clump and Environmental Habitat Variables

Johansson zones are defined by the branching patterns of the host and therefore are a surrogate for grouped branch diameter classes. They are also believed to coarsely represent gradients of other environmental variables such as light and humidity (Johansson, 1974). Indeed, all environmental variables showed significant variation between zones.

Branch Angle

The lower branch angles in Zone 5 reiterate the relationship found between branch angle and branch diameter. It is a testament to the branching architecture and the abundance of drooping outer branches of the *Ficus* and

is contrary to the patterns of branch angle found by Rudolph *et al.* (1998). Figure 27 schematically displays the variation of branching systems in an emergent relative to a generalised canopy tree and describes how low branch angles can be attained in Zone 5 relative to other zones. However, crown architectures vary immensely (see Hallé *et al.*, 1978) and the generalisations made here are coarse. The lack of architectural descriptions of host trees from epiphyte distribution studies hinders comparison.

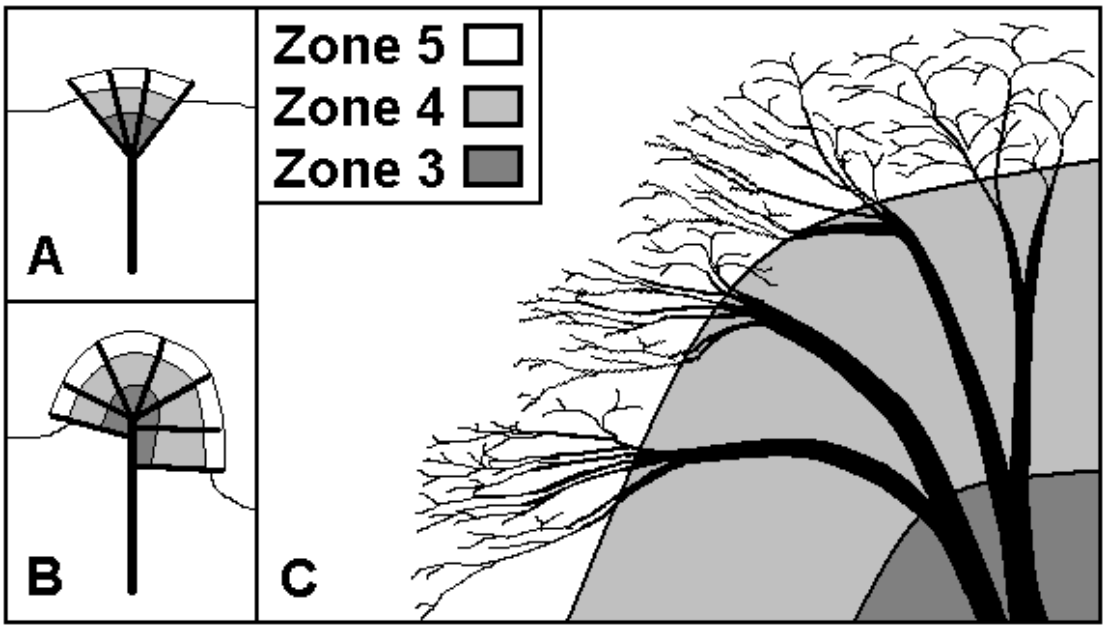


Figure 27: A schematic generalisation of the branching system and Johansson zones of generalised canopy trees (A), emergent canopy trees (B), and the branch angles and Johansson Zones in the outer canopy of the *Ficus* emergent (C).

LAIDev

LAIDev was significantly higher in Zone 2 than Zone 5. This appears to be a result of its high correlation to branch diameter and is likely to reflect the branch structure of the canopy. Clumps on larger branches have a greater proportion of branch area cast into the 180º plane when there is any degree of branch inclination. Thus, in the lower zones, where larger diameters and higher branch angles exist, higher proportions of the sky are shaded by branches that increases the deviation of visible sky obstructions across the image.

VisSky

VisSky is positively related to the amount of incident diffuse radiation, regardless of the sky obstructions along the sun's path. The mean values of VisSky were the same in Zone 4 and 5. Interestingly, they were also the same in Zone 2 and 3. The homogenisation of VisSky within the upper canopy zones is more evidence of the effects of the emergent structure on the Johansson Zones. Were there not such a large lateral element to the canopy surface, VisSky would be expected to decrease from Zone 5 to 2. As is shown in Figure 27 – B, Zone 4 and 5 both occupy similar height ranges.

Zone 2 and 3 did show lower VisSky values than the upper canopy zone. The homogenisation of values within Zone 2 and 3 can be attributed to the increase in canopy holes at high Zenith angles. This is evidenced by both the high LAIDev and morning radiation (RadMorn) in Zone 2.

Photosynthetically Active Radiation

The extinction of radiation by the *Ficus* canopy appeared higher than those reported by ter Steege and Cornelissen (1989) in lowland forest trees. Despite the high radiation available at the leaf tips of a tree crown, all the radiation variables from epiphyte clumps suggest that vascular epiphytes of the *Ficus* host are mostly intolerant of full sun. For one epiphytic bromeliad studied in Panama, radiation in excess of 30% irradiance reduced plant growth (Laube and Zotz, 2003). The selection of grow sites is also highlighted by the range of all radiation variables in Zone 4 and 5 and also seen by the dearth of epiphytes on branch diameters of $\leq$ 1 cm. This may also be related to the long dry season.

The distribution of all radiation variables in the Johansson Zones did not follow an even trend. The radiation receipt at Zone 3 was the lowest of the zones. However, the radiation receipt at Zone 2 was higher than in Zone 3. This can be explained by the relatively high exposure of the lower canopy at high zenith angles as evidenced by the relatively high RadMorn in Zone 2. Heterogeneity of light conditions in the lower canopy zones was also found in a lowland forest by ter Steege and Cornelissen (1989). It is also important to note that Zone 3 locations may have a higher extinction of radiation due to

the proximity to multiple vertical branches on many aspects. By comparison, Zone 2 locations receive heavy shading by the trunk in either the afternoon or the morning that also results in a higher LAIDev.

4.4.3.3 Floristics

Lifeform and Taxonomic Groups

The occurrence of all common lifeform and taxonomic groups across all zones was indicative of a large amount of floristic overlap between zones. Freiberg (1996) had previously reported that the lifeform classification of Hosokawa (1943) was only slightly useful for distribution and that a revision was in order. In the present study, modifications to the Hosowaka epiphyte lifeform classification were made that were based on the characteristics of the local epiphyte flora and intuitive decisions. The usefulness of lifeform and taxonomic groups is enhanced in diverse mesic environments where most species are not sufficiently abundant to be tested statistically. Most common lifeforms did show variation in abundance between the zones.

Lepanthid orchids, especially of the species rich genus *Lepanthes*, are an interesting and distinct ecological group. They are very small and flower continually year round (Luer, 1996, 1997), commonly colonise bare substrate on trunks (Catling and Lefkovitch, 1989) and yet the individual species are often very sparsely distributed (Tremblay, 1997). Despite the sparse distributions of species, the creation of the lepanthid lifeform group was able to statistically display their preference for the trunk environment.

The split of the creeping habits into ferns and angiosperms (fern – creeping, angiosperm – repent) was also of use. Long creeping ferns were shown to perform well in the lower canopy, while long repent angiosperms performed better in the upper canopy, and the latter were particularly poorly represented in the low light of Zone 3. Similarly, the short creeping ferns appeared to prefer higher PAR and their distribution followed the zone patterns for PAR distribution. Again, short repent angiosperms were the reverse of the fern equivalent and showed a preference for the low light and sparse cover of Zone 3.

The taxonomic groupings also appeared useful. The preference for lower canopy conditions by ferns and herbs could be shown statistically. Likewise, the preference for upper canopy conditions by orchids and bromeliads could also be shown. The creation of the pleurothallid group highlighted the significance of this orchid subtribe. Without separation from the family, this neotropical phenomenon might disguise the general trends of all other orchids by their tolerance of a wide range of conditions and their large number and diversity. This was evidenced by the very high PA's in all zones, particularly in the lower canopy, contrary to all other orchid patterns.

The above trends are common in neotropical areas and, were interestingly, the same as those found in Gabon, where some ferns and Araceae were restricted to trunks, while orchids predominated in the outer canopy (Engwald *et al.*, 1999).

Epiphyte Species

The significantly varying distribution patterns of the majority of epiphyte species reflected two main differences in epiphyte habitat. The first is the distinction between the upper canopy and the trunk, and the second is the distinction between shade habitat and sun habitat. This distinction of sun-shade epiphyte habitat provides niches for epiphytes with different PAR requirements/tolerances (Griffiths *et al.*, 1984).

The difference in habitat characteristics between the upper canopy and trunks are large. Trunks and upper branches require different strategies of attachment. Many of these examples were not shown statistically due to the low abundance throughout the entire tree of the species restricted to trunk habitats. The most profound of these examples are the hemiepiphytic and holoepiphytic climbers. Most of these species are completely restricted to Zone 2 (Williams-Linera and Lawton, 1995) (and therefore low in relative clump frequency), with some having achieved their life goal of reaching the humus deposit of the main fork of the tree at the base of zone 3. Their persistence further up vertical canopy branches is probably restricted by their lack of adaptation for high water stress (Laman, 1995; Mantovani, 1999; Patiño *et al.*, 1999), a likely trade-off for the ability to grow rapidly in order to

climb.

The only common species that could persist in the upper canopy and on the trunk were some *Elaphoglossum* species and the pleurothallid orchids. The latter are a remarkable neotropical group that dominates neotropical epiphyte floras, and many genera are not only particularly species rich, but from the data presented, appear adapted to a wide range of conditions. Of the thousands of species, many have very large altitudinal ranges (Luer, 1986b; Vásquez and Ibisch, 2000). Only one of the seven common pleurothallid species was not found in every zone, and the pleurothallid group was shown to have the highest PA in every zone except for third place in Zone 5. *Elaphoglossum* is also a particularly species rich neotropical genus that shows a wide range of adaptations, and commonly displays phenomenal morphological variation within species (Mickel, 1980, 1985).

The lack of bromeliads in Zone 2, appeared to be related to the limitations of their method of attachment. Many tank bromeliad species establish a large attachment that completely encircles canopy branches in order to suspend and balance their large weight of water. Though not limited by lower light levels found in Zone 2 (Griffiths *et al.*, 1984), large mesic tank bromeliads have no way to support themselves and their mass of water on smooth bark without a branch small enough to encircle, or flat and wide enough on which to balance. The smooth barked *Ficus* trunk presents quite an obstacle to Bromeliaceae sp. 1 and sp. 2, both of which had rosettes with over one meter diameters and must have weighed at least 30 kg at maturity (Zotz and Thomas, 1999).

The absence of the majority of orchids from Zone 2 is also likely to be a response to their lack of adaptations for trunk attachment or to the lack of canopy humus and high PAR. Most orchids find it easy to attach themselves to thin branches that are easily encircled by their water imbibing roots (Benzing, 1990; Benzing *et al.*, 1983). They and many other upper canopy specialists such as bromeliads have a high light demand/tolerance (Benzing and Renfrow, 1971; Haslam *et al.*, 2003; Hietz and Briones, 2001; Stancato *et al.*, 2002) and many common species appeared just as intolerant to the

shaded conditions of Zone 3 as to those of the trunk. Light demand may be an important factor in explaining the epiphyte distribution pattern in the present study. In lowland forest, the outer canopy presents a fierce environment, where temperatures soar into extreme ranges for vascular plants in the absence of cloud. However, in the montane cloud forest of the present study, temperatures during the day rarely climbed above 20 Cº, high cloudiness is the norm and canopy humus rarely has a negative water balance during the wet season. Under these conditions, the outer canopy would appear comparatively mild.

4.4.4 Floristic Ordination

The ordination and ANOSIM results reflect the contrasts in floristic composition of the Johansson Zones and along branch diameter gradients. There are few published accounts on the species associations of canopy epiphyte clumps. Many studies use epiphyte cover and biomass. Bøgh (1992) used a TWINSPAN analysis to analyse the composition of the Johansson Zones ("stands") throughout the canopy in a 175 m^2 plot. He found three large groups that reflected the height distribution of the zones. The height distribution of the individual species was larger than that of the floristic groups. Despite, the shortcomings of TWINSPAN (McCune *et al.*, 2002), the results show some similarity to those of the present study, in that Johansson Zones (surrogate for height) have different floristic compositions, despite a heavy overlap of species distributions between zones. The only other example of floristic analysis of epiphyte communities was that of Catling and Lefkovitch (1989) who used conditional clustering to analyse epiphytic associations using whole understorey trunks (3 m height) as subplots. They identified an association of lepanthid orchids with a colonising role.

Despite the moderately high stress value in the current ordination, a high confidence can be placed in the solution. The high stress value is a result of the immense sample size and number of species. A large sample size always tends to increase stress levels in any dataset (Clark, 1993). Sometimes this increase can be dramatic as demonstrated by McCune et al. (2002) using data from 5 to 50 subplots of non-vascular epiphytes

communities. The present ordination uses 606 subplots. Furthermore, Kruskal and Wish (1978), the former being the author of the original stress formulae, emphasised that stress values were of little importance to confidence when the number of objects, *I*, are greater than 4 times the dimensionality, *D*, ($I > 4D$). In the present ordination using 195 species, $I = 65D$.

The broad overlay seen in the ordination plots describes a wide variety of mixed species associations within the upper canopy zones. This tends to suggest that many associations might be by chance rather than through species-specific coexistence or habitat niches.

By comparing the overlay plots of all the variables on all axes (not all shown), the usefulness of the Johansson zonation scheme in this epiphyte habitat could be seen. This variable showed by far the best fit to the clump arrangement within the ordination (Figure 25). The zone variable in the analysis is an ordered categorical variable (2-5) that does not comply with the assumptions of vector fitting. However, the natural ordering of the categories (trunk to outer canopy), and the gradients of many variables that commonly occur along that order, made it an interesting inclusion for comparison to individual variables. Not surprisingly, Johansson Zone returned the highest vector of maximum correlation. Despite having a larger value range (2-110 cm, 1 cm categories), and displaying variation within Johansson Zones (Table 8), branch diameter returned a maximum correlation value very close to Johansson Zone. Whilst the floristic composition of epiphyte clumps has not been previously tested with branch diameter, a wealth of studies have identified species-specific relationships (Freiberg, 1996; Johansson, 1974, 1975; Johansson, 1978; Pupulin *et al.*, 1995; Rudolph *et al.*, 1998). The vector fitting clearly indicates that branch diameter is the most effective stand-alone explanatory variable for the floristic associations measured in the present study.

The ANOSIM test displays how the floristic composition of clumps shows a gradation from zone to zone, with a higher similarity in adjacent zones and a higher dissimilarity between the zones furthest apart. Zone 2 was by far the most dissimilar of all the zones. The similarity to its adjacent zone

was by far the weakest similarity of all the adjacent relationships. This highlights the difference in trunk species compositions compared to the upper canopy zones as partly seen in the contingency table. Together these results reflect and strengthen the above-mentioned differences between trunk and canopy environments. The similarity between the adjacent upper canopy zones was high and reflects the large overlap seen in the ordination plot, and the similarity of species composition in the contingency table.

4.5 Conclusion

It has been established that epiphyte distribution and diversity is markedly concentrated within the outer reaches of the *Ficus* crown. This appears to be a result of the structural attributes of the host. This suggests increasing heterogeneity in the distribution of successional communities with increasing branch diameter. The majority of upper canopy species are flexible in their habitat preference. The upper canopy provides a small amount of niche diversity through the highly variable distribution of PAR and branch angles. The range of epiphyte associations within clumps is very diverse, and species coexistence appears to be very high. The distribution of associations shows a heavily overlapped graduation from the outer canopy to the top of the trunk (Zone 3). The large humus deposit at top of the trunk likely represents a unique habitat worthy of its own zone. The trunk environment differs markedly in its floristic composition compared to the upper canopy as a result of sharp differences in structural and environmental habitat characteristics.

The incredible diversity of species in the *Ficus* host can only be partly explained by the diversity of habitat and structural characteristics. The distribution of epiphyte individuals and species within the canopy is as remarkably different to other studies as is the diversity of epiphyte species. However, the pattern of outer canopy thickening is not entirely explained by the geometric and radiative factors thus far presented. The present study is not the first study within a canopy emergent, nor a tall *Ficus* host, but is the first of this combination in a Peruvian forest on steep slope and high elevation. This environment had yet to be investigated for canopy microclimate. Authors

commonly described the link between canopy microclimates and epiphyte distribution (Freiberg, 1997; ter Steege and Cornelissen, 1989), which may shed more light on the above-mentioned patterns of distribution.

Chapter 5 Canopy Microclimate

5.1 Aims

This chapter describes the microclimatic conditions within the montane forest canopy in order to accomplish the third research aim.

3. Determine the microclimatic profile of the canopy

Studies of vertical microclimatic profiles in tropical forests are rare. Within any type of tropical montane forest, studies of canopy microclimates are very few (Grubb and Whitmore, 1966, 1967; Odum *et al.*, 1970; Pentecost, 1998). The majority of microclimatic canopy studies have been undertaken in tall lowland forest with defined and evenly distributed canopy stratum, a common feature of lowland forests worldwide (Leigh, 1975). These studies find constant gradients of humidity, temperature and light from the canopy top to the forest floor (Engwald *et al.*, 1999; Freiberg, 1997; Kira and Yoda, 1989; Mantovani, 1999; Szarzynski and Anhuf, 2001) and have led to a consensus on canopy microclimates in closed canopies.

However, the tropical montane forest of the present study has a vastly different canopy structure. It is found mostly on steep slopes and is characterised by a very heterogenous canopy stratum due to frequent landslides and treefalls (Figure 28). Assumptions of canopy microclimate based on microclimatic theory from the canopies of taller and more structurally even forests from warmer climates may not be applicable to tropical montane forest. This difference in canopy structure prompted the current research. This chapter is one of the first descriptions of canopy microclimate from a high altitude tropical montane forest. The research aim is achieved by analysing temperature, PAR and relative humidity from a vertical canopy transect installed in the *Ficus* host. The transect represents all canopy zones in which epiphytes are found.

Figure 28: Tropical montane forest canopy on a steep slope.

5.2 Methods

In order to assess the distribution of temperature within the canopy, vertical temperature profiles for February 2004 were obtained from a vertical transect within the *Ficus* emergent. The above canopy conditions (AbCan) were measured from the 18 m canopy tower at a distance of 70 m from the vertical transect. Temperature and PAR were measured at four sites at 10-metre intervals in Johansson (1974) zones along the vertical transect (Figure 29). The 32 m site was located between the convergence of Zone 4 and 5, the 22 m site was located in Zone 3, the 12 m site was located near the upper section of Zone 2, and the 2 m site was at the base of Zone 2. The 32 m and 22 m sites, and the 12 m and 2 m sites are collectively referred to as the upper canopy and lower canopy respectively.

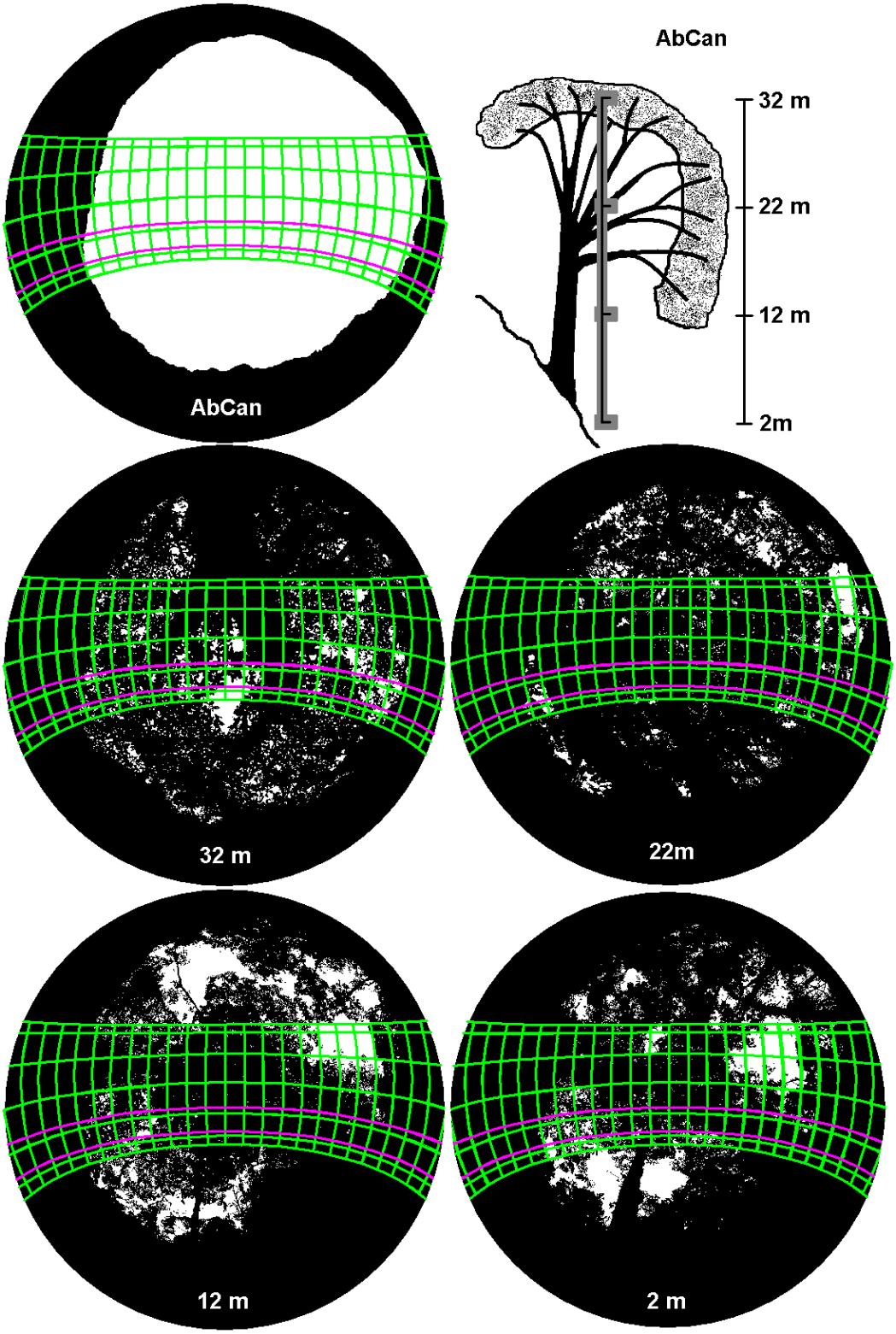


Figure 29: The vertical canopy transect map (top right) and the visible sky proportions at each site. The above canopy (AbCan) temperature was measured on a canopy tower. The matrix indicates the suns path across the sky. Pink lines indicate the suns path in February. Images are classified to grey scale and aligned east-left west-right north-top south-bottom

ACR Jr Info Loggers were used to record temperature for a 5-month period at the three upper sites. These recorded measurements every 2 minutes. For the final month (February 2004), temperature and humidity were also recorded on the forest floor (2 m site) using a second CR10 datalogger and CS500 probe at a resolution of 2 minutes, similar to that on the canopy tower (see Section 2.2.4). The shielded loggers were suspended from a custom-built counterweight rope attachment and were moved along the vertical transect with a rope and pulley system. This allowed weekly inspections, calibrations and downloading from sensors without accessing the canopy. Twenty minutes of data were lost each week in order to lower the transect and download the stored data from the loggers. Sensors were suspended in locations more than 50 cm from branches. Relative humidity was also measured above the canopy and at the forest floor.

Hemispherical images were taken to assess PAR at each sensor location. All PAR calculations were made with HemiView (Delta-T Devices Ltd., 2001). Two calculation models were used. The February model was based on February PAR data taken directly from the PAR sensor at the canopy tower. The annual model was based on annual PAR data. Each model therefore represented the transmissivity (cloudiness) of each period. PAR calculations included DIRECT PAR (February), YEAR DIRECT PAR (whole year) and TOTAL PAR (direct + diffuse for whole year).

5.3 Results

5.3.1 Temperature

The daily temperatures at the vertical canopy transect in February (Figure 30) show a lower day average and a higher night average than the annual averages for the study site (Figure 31). This is typical of wet season patterns due to increased cloudiness. The depression in the temperature curve of all sites around 1:00 pm is an artefact of the high cloudiness of the site and the short time series. The canopy temperature profiles (Figure 32) describe the large amelioration (c. +1 °C) of noon temperatures by the canopy. Day temperatures on the profile were characterised by the minima

in the upper canopy, and the maxima above the canopy. During the night, the canopy surface ameliorates cool temperatures by c. 0.5 °C. Nocturnal temperatures on the profile were characterised by minima on the forest floor and above the canopy, and maxima in the upper canopy. All sites briefly showed equal temperature at 6:00 pm as the temperature profile reverses.

In the lower canopy, the 2 m site had the coolest nocturnal temperature on the profile and was the quickest to cool in the afternoon. It appeared to cool at the same rate as above the canopy into the early evening, but continued to decline steeply after the upper canopy began to level out around 7:00 pm. During the day, the 2 m site remained cooler than the site at 12 m, with the exception of a brief period at around 10:00 am. The 12 m site was the warmest location on the profile during the day and at night was slightly cooler than those sites in the upper canopy.

In the upper canopy, the 22 m site was the coolest on the profile at noon, and in the evening, was slightly cooler than the upper site and warmer than those sites in the lower canopy. The 32 m site appeared the most amiable over an entire day for vascular plants. At night, the 32 m site is the warmest, and during the day, is similar to the coolest 22 m site and is cooler than the sites at 12 m and 2 m.

The maximum positive temperature deviations of canopy sites from above canopy conditions highlight the difference between the upper and the lower canopy sites (Table 11). Upper canopy sites are higher at the peak of nocturnal minimum temperatures, whilst lower canopy sites are higher at the commencement of nocturnal cooling. The 2 m site had the lowest average temperature and the highest temperature deviation, while the 22 m site had the lowest temperature deviation (Table 12).

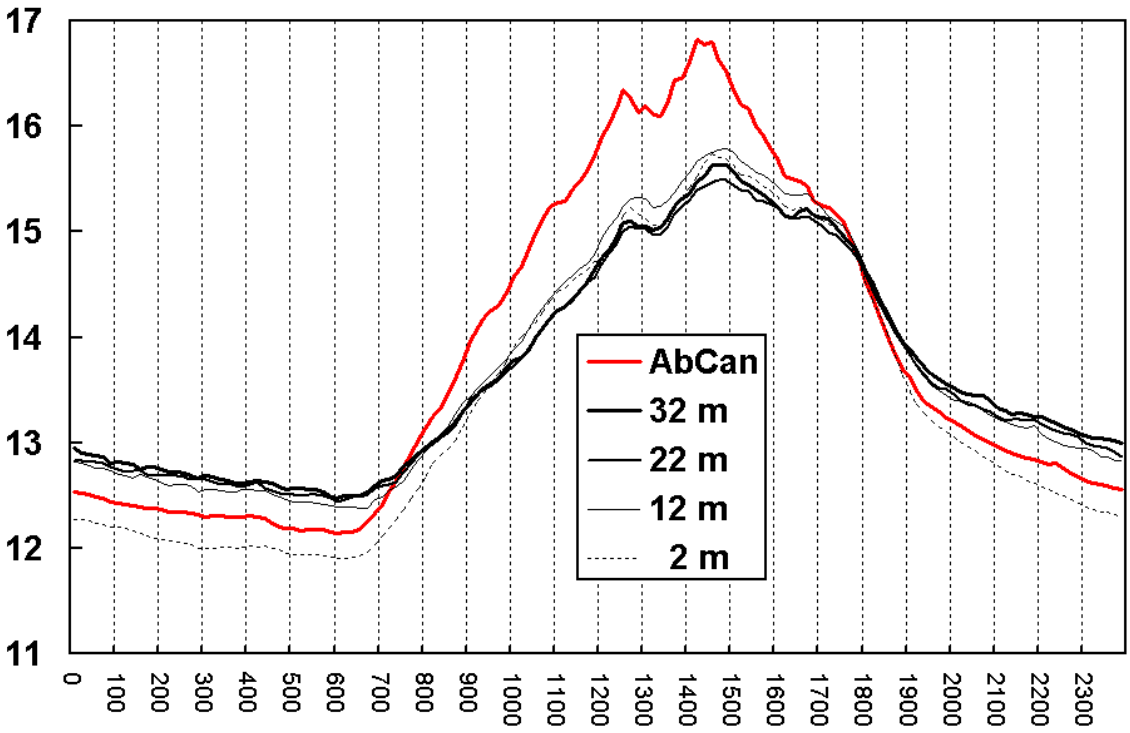


Figure 30: A 24-hour time series of 10-minute temperature averages (°C) from above the canopy (AbCan) and four canopy heights from the forest floor for February 2004.

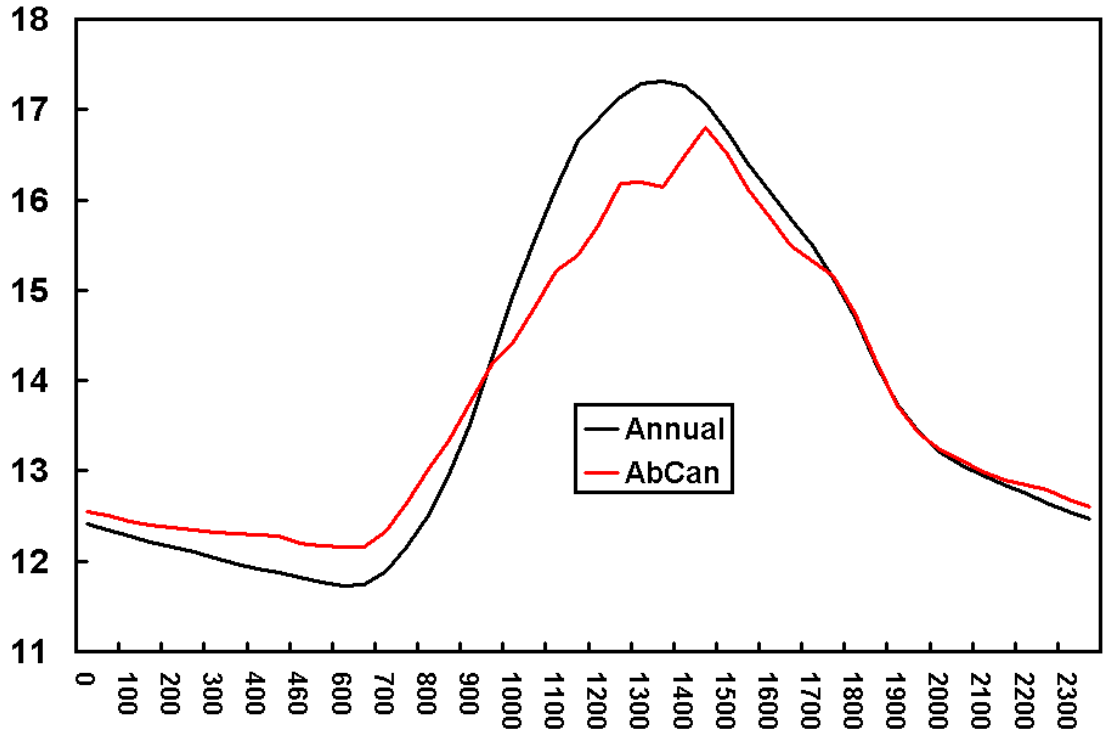


Figure 31: A 24-hour time series of 30-minute temperature averages (°C) from above the canopy for 2003-2004 (annual) and February 2004 (AbCan).

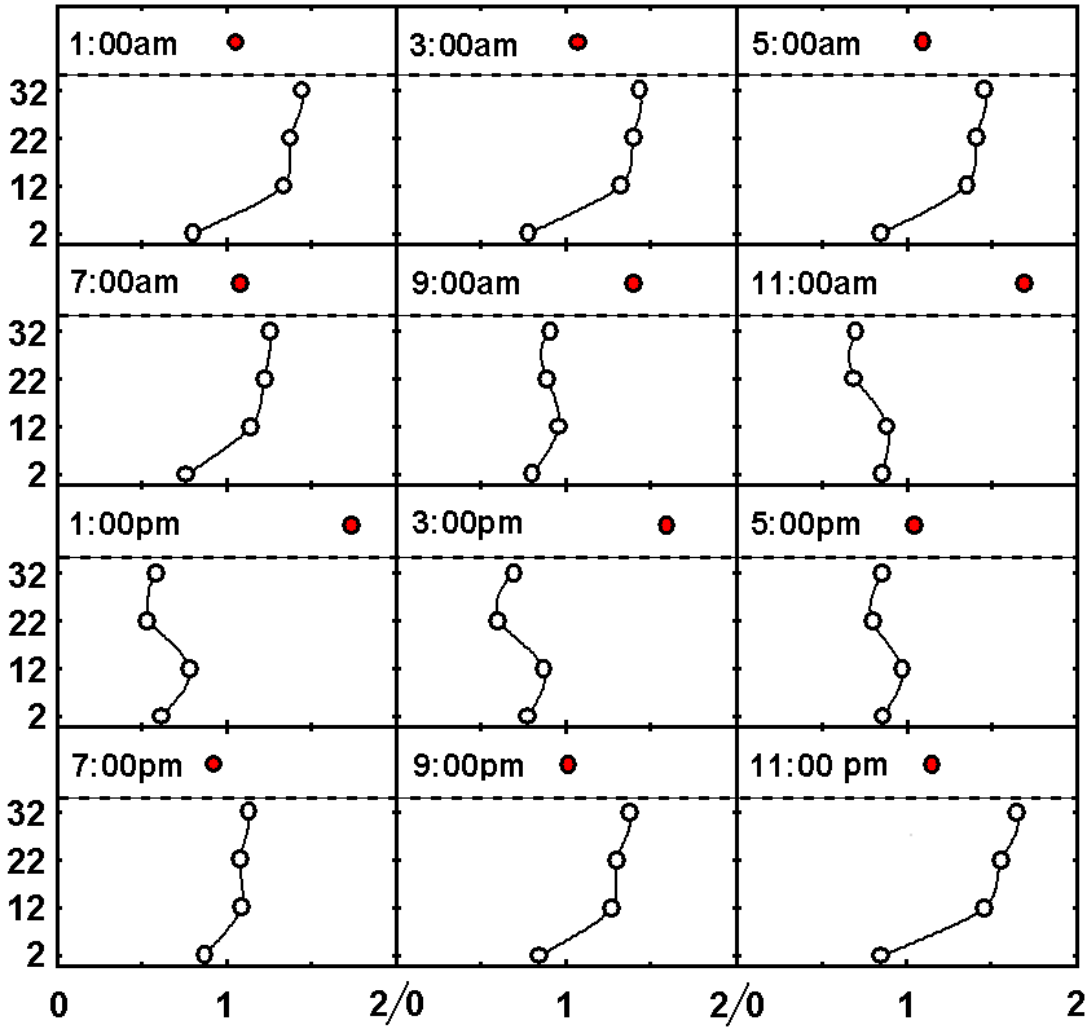


Figure 32: Two-hourly canopy temperature profiles for February 2004. Canopy height (Y) is measured as metres above the forest floor. Temperatures (X) increase in °C from left to right. Shaded circles are the above canopy temperature measured at a distance of 70 metres from the transect. Black dotted lines represents the surface of the canopy. These profiles do not attempt to represent the processors of radiative cooling or radiative heating that occur on the surface of the canopy.

Table 11: Maximum deviation from above canopy conditions in February 2004. Temperatures (°C, $T_{im} - T_{AbCan}$) are in bold text with the corresponding time to the left.

32 m		22 m		12 m		2 m	
6:10 am	**2.27**	6:50 am	**2.08**	4:50 pm	**2.13**	5:00 pm	**1.39**
11:30 am	**-3.49**	11:30 am	**-3.82**	10:40 am	**-3.42**	2:10 pm	**-3.37**

Table 12: Summary of radiation and temperature on the vertical canopy profile for February 2004. VisSky is reported as a fraction. PAR (mol. m^2) figures are totals for the given period. Temperature (°C) deviation is the standard deviation over the February sampling period.

	AbCan	32 m	22 m	12 m	2 m
VisSky	0.60	0.08	0.05	0.11	0.10
DIRECT PAR	928	201	25	52	102
YEAR DIRECT PAR	9853	1583	506	1047	1553
TOTAL PAR	19922	2980	1225	2857	3349
Temp Mean	13.81	13.69	13.64	13.69	13.38
Temp Deviation	1.97	1.54	1.52	1.59	1.78

5.3.2 Relative Humidity

Relative humidity was measured above the canopy and at the forest floor (2 m site). On a few occasions the forest floor humidity was considerably lower than the upper canopy (Figure 33). These occasions coincided with heavy fog events above the canopy at night. Relative humidity was saturated above the canopy for 67% of February. Forest floor conditions were saturated for 73% of February.

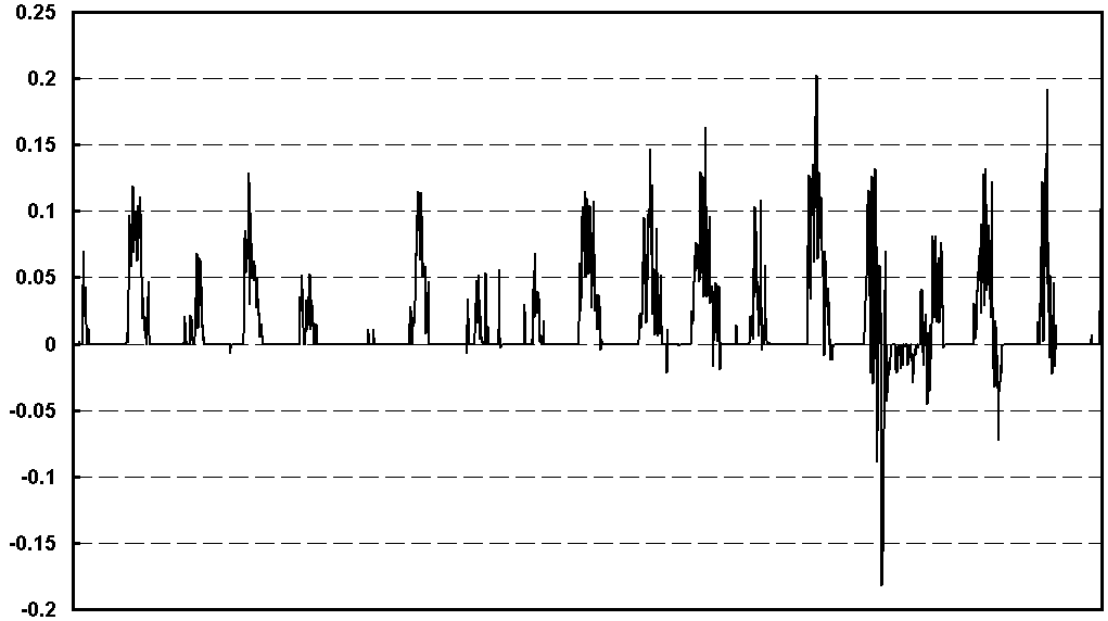


Figure 33: A 19-day time series of the difference in relative humidity (fraction) between above the canopy and the forest floor in February 2004 ($RH_{2\,m} - RH_{AbCan}$).

5.3.3 PAR and Site factors

All canopy sites receive a large amount of shading relative to locations above the canopy (Figure 34, Table 13). Both lower canopy sites receive more DIRECT PAR in the morning when zenith angles are highest. The morning peak of DIRECT PAR at the 2 m site also coincided with a brief period when the 2 m site temperature was the highest on the profile at 10:00 am (Figure 30). DIRECT PAR is briefly high at the 12 m site in the morning. This might be seen to contribute to the high temperatures. However, temperature remains higher at the 12 m site than the 32 m site during the afternoon, despite higher noon and afternoon radiation at the 32 m site. The 22 m site receives very little direct radiation and receives its only significant amount of DIRECT PAR at the highest zenith angle. The 32 m site receives more DIRECT PAR than other canopy locations, receiving little at high zenith angles and its maximum amount at noon.

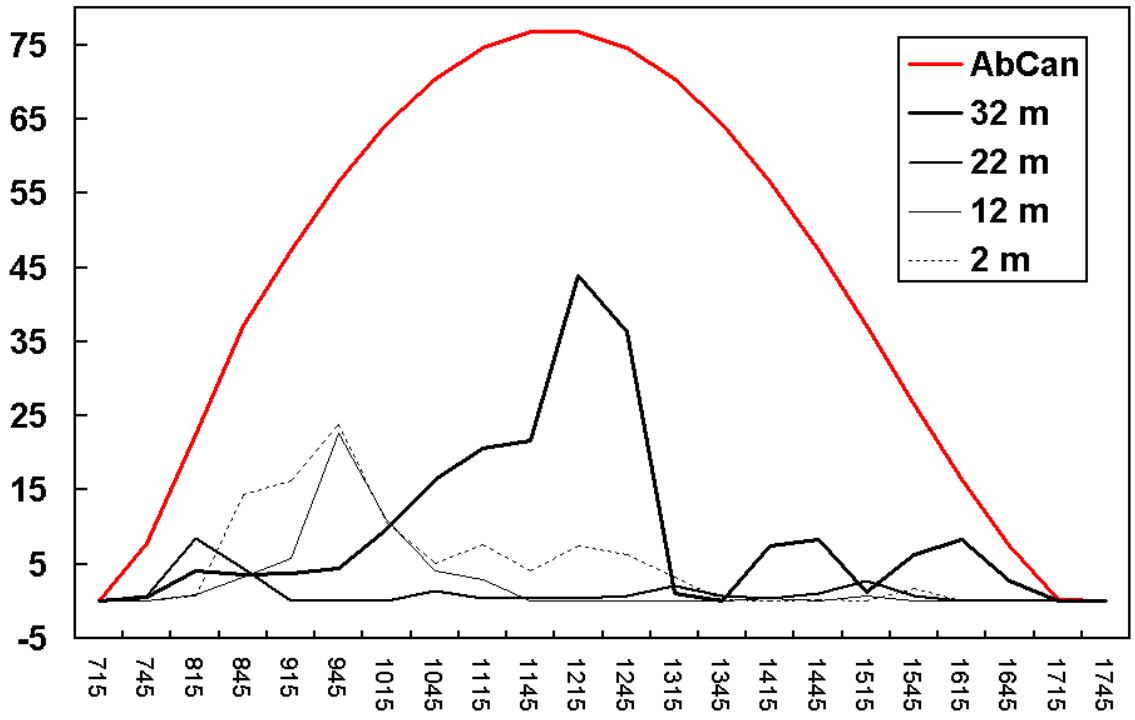


Figure 34: Trends of 30-minute DIRECT PAR totals (mol. m^{-2} min^{-30}) from above the canopy (AbCan) and four canopy heights from the forest floor for February 2004.

Table 13: A summary of 30-minute DIRECT PAR totals (mol. m^{-2} min^{-30}) from above the canopy (AbCan) and four canopy heights from the forest floor for February 2004.

Time	AbCan	32 m	22 m	12 m	2 m
07:45	7.5	0.6	0.7	0.0	0.0
08:15	22.4	4.2	8.6	0.9	0.8
08:45	37.2	3.6	4.5	3.2	14.4
09:15	47.4	3.8	0.0	5.8	16.2
09:45	56.6	4.4	0.0	22.7	23.8
10:15	64.4	9.7	0.1	11.1	10.7
10:45	70.5	16.4	1.4	4.1	5.1
11:15	74.6	20.7	0.4	2.9	7.6
11:45	76.8	21.6	0.4	0.0	4.1
12:15	76.7	44.0	0.4	0.0	7.5
12:45	74.6	36.4	0.7	0.0	6.4
13:15	70.4	1.0	2.1	0.0	3.3
13:45	64.4	0.0	0.7	0.0	0.2
14:15	56.6	7.4	0.4	0.3	0.0
14:45	47.4	8.3	1.0	0.1	0.3
15:15	37.2	1.2	2.8	0.7	0.1
15:45	26.6	6.3	0.7	0.0	1.7
16:15	16.4	8.4	0.0	0.0	0.0
16:45	7.5	2.7	0.0	0.0	0.0
17:15	0.3	0.0	0.0	0.0	0.0

The VisSky fraction of the 12 m site is the highest of all canopy sites. The 22 m site has by far the lowest VisSky fraction. The YEAR DIRECT PAR is highest in the canopy at the 32 m site and the 2 m site and lowest at the 22 m site. TOTAL PAR is highest in the canopy at the 2 m site and lowest at the 22 m site. The high TOTAL PAR in the lower canopy relative to respective YEAR DIRECT PAR is a result of a higher amount of diffuse radiation that accompanies a higher VisSky value.

5.3.4 Clear Sky and Rain Events

The canopy profile changed under different climatic conditions, as illustrated by a continuous 48-hour period with contrasting conditions in Figure 35. The first 24 hours is affected by both a nocturnal (1) and day (2) rain event. The second 24 hours is a relatively clear period for wet season conditions. The rain event 1 registered 11.6 mm over a 6-hour period. The

rain event 2 registered 12.7 mm over an intermittent 4.5-hour period. The first 24-hour period showed a c. 5.5 °C rise above the canopy from 6:00 am to 2:00 pm with a canopy range of c. 4 °C. This is compared respectively to c. 11.5 °C and c. 8 °C over the same period in the following 24 hours.

Under all sky conditions, temperatures drop rapidly from 5:00 pm, levelling out at around 8:00 pm to decline steadily at a lower rate. Under clear sky conditions, nocturnal temperatures decrease more steeply in the 2 m and upper canopy site than the other sites. The 32 m and 22 m sites are c. 1.75 °C warmer at the peak of night minima at 6:00 am. Under clear sky conditions temperatures rise sharply and at 9:00 am, there is a brief period where all sites are equal. There are some sharp depressions (c. 2 °C) in the day above canopy temperature curve of the 27th February caused by cloud but all canopy sites showed a very damped reaction (c. 0.5 °C). The 32 m and 22 m sites are the warmest locations in the canopy though c. 2 °C less than above the canopy under full sun. At around 5:00 pm, another brief period passes where all sites are equal before the above canopy and 2 m site temperatures fall below those within the canopy.

Rain and mist events changed the temperature profile in the canopy. Preceding the evening rain event by an hour was the arrival of heavy mist that reverses the cooling trend (1). As the rain commences, cooling resumes but the minimum temperature increases. At the highest intensity of rain, the temperature profile is completely homogeneous. This effect appears to last for several hours after the rain passes. In the next morning, as the atmosphere warms, the clear sky profile is reversed and the upper canopy is the coolest as the atmosphere warms. After the next midday rain event (2), maximum temperatures and canopy gradients are reduced. In the evening after the rain events, the two upper canopy sites are considerably warmer than during the previous evening.

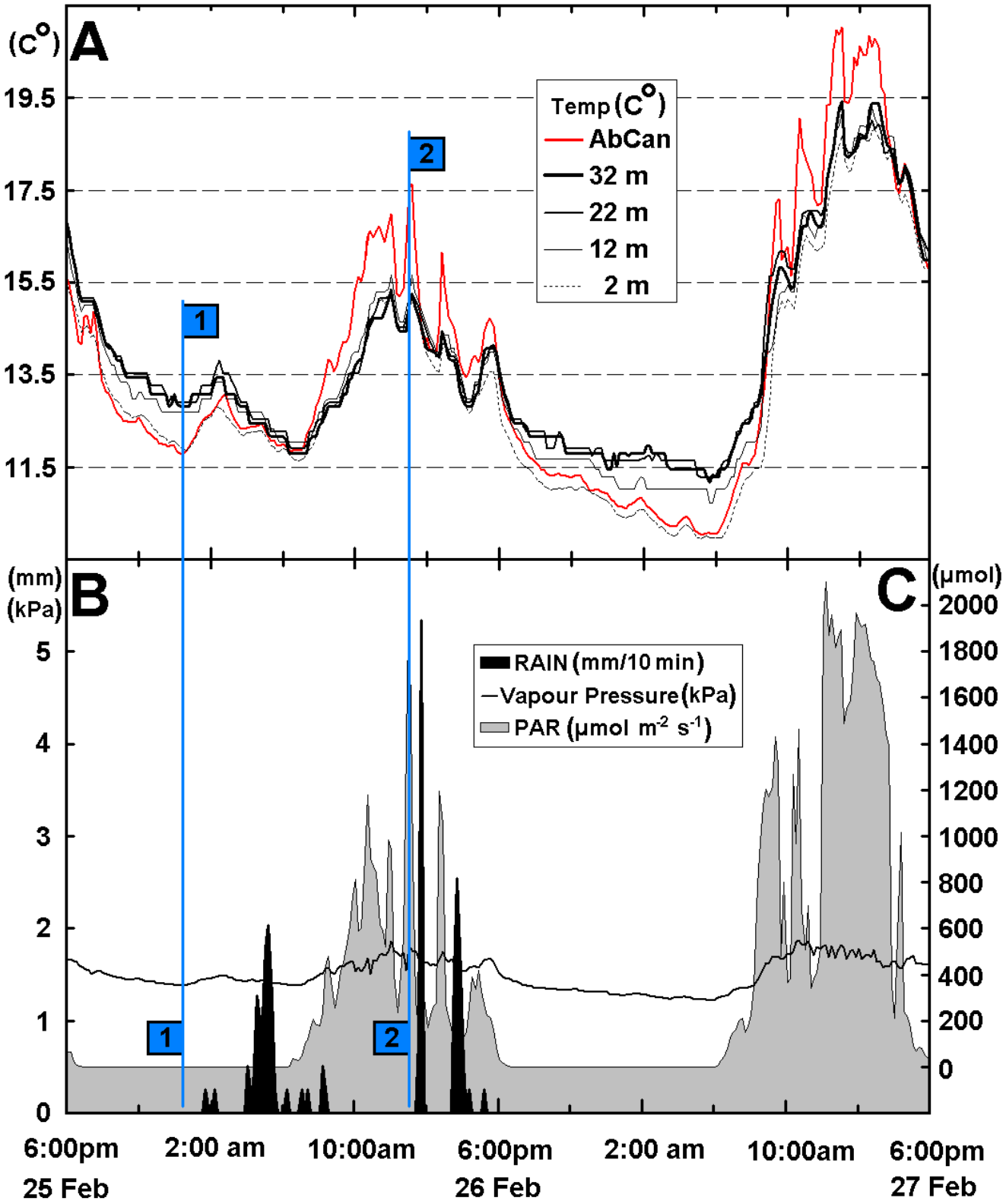


Figure 35: A 48-hour time series of temperatures (A) at five heights from the above the canopy (AbCan) to the forest floor (2m), rainfall and vapour pressure (B), and photosynthetically active radiation (C). The blue lines marked as 1 and 2 signify the start of rain events.

5.4 Discussion

The results from the vertical transect indicate that the canopy microclimatic profile of tropical montane forests is markedly different from that typical of tropical lowland forest. The upper canopy was particularly equable, and the lower canopy was particularly variable. This can be attributed to two phenomena. The first is the distribution of epiphytic growth and canopy humus deposition, which alters particular canopy microclimates, and the second is canopy structure, which affects airflow within the canopy.

5.4.1 Modification of Microclimate by Epiphytes

The amelioration of canopy temperatures and humidity by canopy humus and epiphytes is described by both Freiberg (2001) and Stuntz *et al.* (2002). Freiberg (2001) showed that at night, temperatures close to branches were increased in the presence of canopy humus because of the reduction in radiative cooling, and that epiphytes generally reduce air circulation under day or night conditions. This effect was detected at 12 cm from branches but not at 75 cm. During the day, Freiberg (2001) found that evaporation from canopy humus reduced temperatures close to branches by up to 4.8 °C. Stuntz *et al.* (2002) found the same effect as Freiberg (2001) for temperature during the day, and also that water loss in the air adjacent to epiphytes was reduced by 20%. These ameliorating effects are the result of the water retention by the epiphytic accumulations. Epiphytic accumulations, and some of the plants themselves (tank bromeliads), suspend large quantities of water in the canopy for long periods after rain and mist events (Bohlman *et al.*, 1995; Kurschner and Parolly, 1998b; Richardson *et al.*, 2000; Veneklaas *et al.*, 1990; Zotz and Thomas, 1999). During the day, evaporation of this moisture reduces temperature, whilst at night, the heat capacity of water reduces radiative cooling.

Here, it is believed that the concentration of epiphytes in the outer canopy zone (32 m site), as shown in the previous chapter, significantly affects the canopy microclimate. The previously mentioned studies were undertaken where epiphytic distributions were concentrated towards the inner

crown of trees, where the air space between other branches was large. Because branches, and therefore epiphyte communities, were more densely arranged in the outer canopy, the air space between communities was relatively small. Freiberg (2001) found that at 75 cm there was no ameliorating effect. Yet, in the outer canopy of the *Ficus* tree, there is rarely 75 cm of open space. Therefore, the day and night ameliorating effects of epiphyte communities affect not only *in situ* branch conditions, but also the canopy microclimate, as evidenced by the temperature profile. It is therefore proposed that the capture and retention of moisture and the reduction of airflow by the outer canopy epiphyte community is responsible for a previously undescribed type of temperature profile in the upper canopy. This conclusion is reinforced by the lower temperatures in the upper canopy during the atmospheric warming before rain event 2, an effect that was likely to be caused by the canopy being saturated after rain event 1 (Figure 35).

5.4.2 Modification of Microclimate Profile by Forest Structure

Another abnormal feature of the temperature profile was the higher day temperatures below the tree crown, and the cool night temperatures found on the forest floor. This is explained by canopy structure. The 12 m site was found just below the crown of the emergent tree (Figure 29), yet above the ground vegetation. The high temperatures found at the site, despite the shading from above, are likely a result of the increased airflow at the site as evidenced by the high VisSky value. This is a feature of broken forest canopy structures on slopes, where the penetration of direct radiation and wind can occur non-vertically (Walter and Torquebiau, 2000) through the increased surface roughness of the canopy. This penetrability was evidenced by the temporal element in the penetration of direct PAR within the canopy. At high zenith angles, lower canopy locations receive more direct PAR than the dense upper canopy, also illustrated in the hemispherical images (Figure 29). The sites above and below have cooler day temperatures due to the protection offered by the dense tree crown and understorey vegetation respectively. The penetration of direct radiation to lower parts of the montane canopy is a known phenomenon (Grubb and Whitmore, 1967) and has been assumed to

increase epiphyte diversity in lower canopy levels of montane forest (Bøgh, 1992). In the present study, the trunk housed the lowest abundance of epiphytes due to the difficulty of attachment, though the diversity of species by some alpha diversity indices was the highest.

In a tall closed canopy, understorey night temperatures are most always the warmest, as the closed canopy above provides thermal insulation (Fitzjarrald and Moore, 1990; Szarzynski and Anhuf, 2001). At the canopy surface in lowland forest, radiative cooling forms a cold air layer that creates an inversion above the canopy (Fitzjarrald and Moore, 1990). Under still conditions, the loss of long-wave radiation from the understorey is reduced by both the presence of the canopy, and, the decoupling of canopy and atmospheric air masses by the inversion layer at the canopy surface (Szarzynski and Anhuf, 2001). However, in montane forest on steep slopes, closed canopies are rare. On steep terrain, forest canopies are not perpendicular to the forest floor and are often subject to higher rates of tree mortality (Bellingham and Tanner, 2000; Hallé *et al.*, 1978) and landslides (pers. obs.). This increases the canopy surface roughness and air turbulence within the canopy, and, therefore, the mixing of canopy and atmospheric air masses is increased. This prevents the decoupling of the canopy and atmospheric air masses, and long-wave radiation from the understorey may escape through the frequent sky gaps in the canopy. This increased radiative cooling on the forest floor will lower understorey temperatures. In the upper canopy, long wave radiation can be trapped by the fragmented outer canopy, especially if laden with epiphytes. However, this process alone cannot explain the very cold temperatures found on the forest floor.

Figure 36 is a schematic representation of the distribution of nocturnal temperature in lowland forest based on previous findings, and the hypothetical distribution of temperature in steep sloped montane forest based on the present study. In the closed canopy of the lowland forest, an inversion layer is created at the canopy surface by radiative cooling effects. This is maintained by the integrity of the canopy until rain, mist or wind events create sufficient turbulence to destroy it (Fitzjarrald and Moore, 1990). In the montane forest, radiative cooling must still occur at the canopy edge, but can an inversion

be maintained when the canopy is characterised by emergent trees (Figure 28), especially when the below crown surfaces are loaded with epiphytes that appear to slow the loss of long-wave radiation? Here it is suggested that the product of radiative cooling on the canopy surface must drain down to the understorey through the frequent sky gaps of the heterogenous canopy (Figure 36). This would create a flow of very cool air to the forest floor in specific and heterogeneously distributed locations. In this situation, forest floor temperatures in certain locations may reach minima below that of the atmosphere due to *in situ* radiative cooling and the influx of cool air from canopy radiative cooling. Forest floor nocturnal temperatures would therefore be expected to vary on horizontal transects throughout montane forest with high surface roughness. Such distributions of nocturnal temperature may have significant influences on the distribution of understorey vegetation. This could influence the relatively higher diversity of shrubs and bushes commonly found at higher altitudes (Grubb *et al.*, 1963).

The heterogenous canopy of montane forest on steep slopes is likely to have impacts on forest-scale ecosystem budgets. The increase in turbulence within the canopy, is likely to increase efficiency of both cloud water capture by vegetation (Asbury *et al.*, 1994; Cavelier *et al.*, 1997; Clark *et al.*, 1998c; Sugden, 1981), and downward flow of moisture. The high surface roughness is likely to considerably increase the radiation receipt of the forest by exposing a greater surface area of vegetation (Grubb and Whitmore, 1967). This occurs, as at high zenith angles, a much higher proportion of horizontal surfaces will encounter incident radiation, relative to a flat forest. Likewise, this may be ameliorated if the aspect creates a shading effect. A strong seasonal element that highlights the effects of slope on forest structure could also be seen in the PAR results. The 2 m site has an equal amount of yearly total direct PAR as the 32 m site, yet in February, the 2 m site total was only half. This suggests that for tropical forests on steep slopes, canopy profiles, and the plants within them, are subject to seasonal variation in the penetration of direct radiation due to the influence of the zenith. The importance of zenith angles is not usually considered in the tropics.

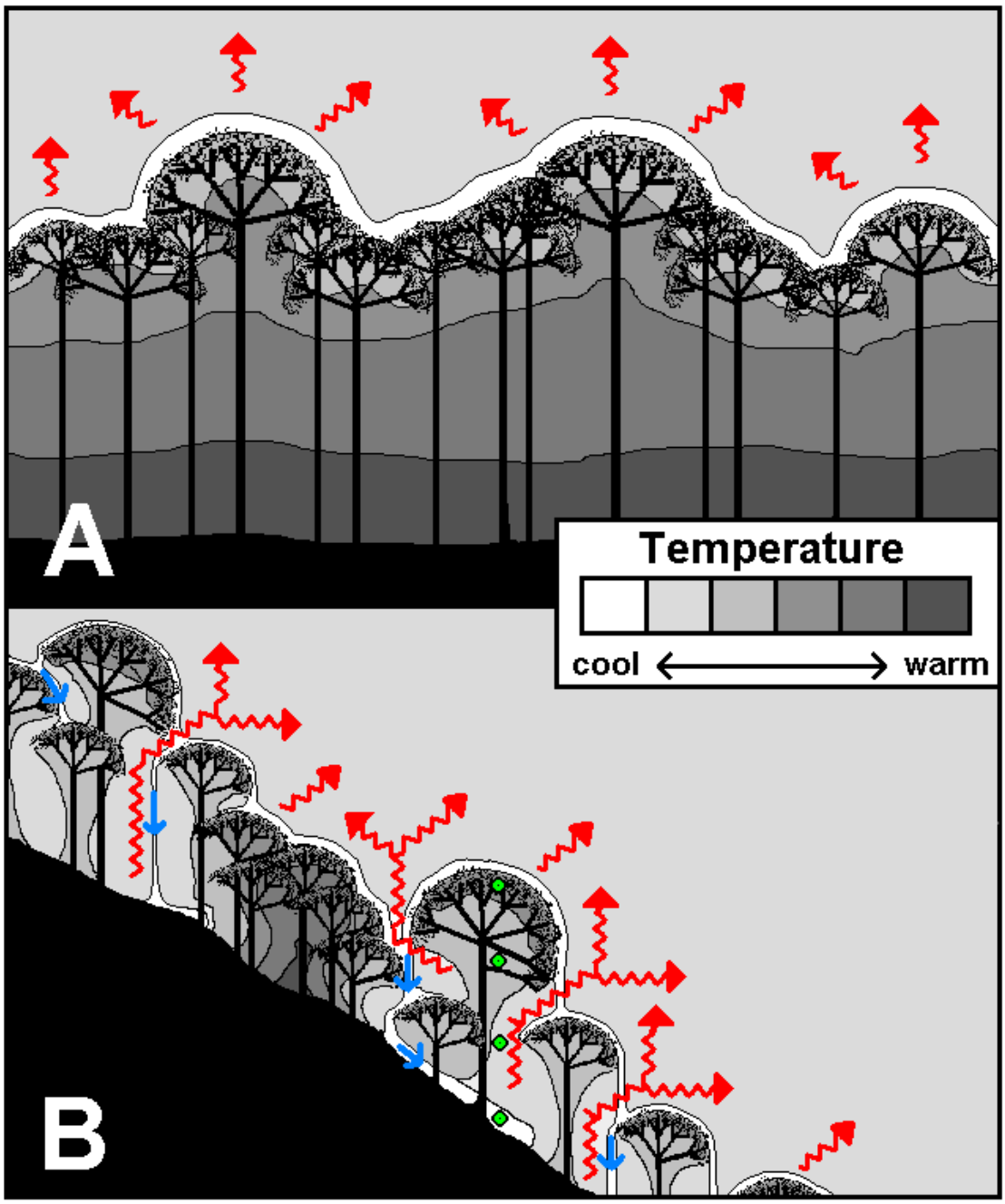


Figure 36: A cross section of canopy structure and distribution of nocturnal temperature at a lowland forest (A) and the montane forest of the study site (B). The white areas of cool temperature are created by radiative cooling at the canopy surface. Red arrows represent the loss of long-wave radiation and blue arrows represent the downward flow of cool air from radiative cooling. Green circles are the sites along the canopy transect from the present study.

5.4.3 Modification of Microclimate Profile by Clouds and Mist

The effect of mist and rainfall on the canopy profile was considerable. Rainfall events are known to decouple canopy profiles rapidly in both day (Fitzjarrald *et al.*, 1990) and nocturnal conditions (Fitzjarrald and Moore, 1990) in Amazonian rain forest. In the day rain event 2, the almost instantaneous homogenising of the profile was observed. During that afternoon, all three upper sites fluctuated in a completely homogenised state until the evening. The exception was the understorey that was noticeably slower to react to the sharp bursts of sunlight. During the day in Amazonian forest, the recovery of profiles can take over an hour at midday (Fitzjarrald *et al.*, 1990). In the cooler montane forest, where epiphytes are present in the upper canopy, the recovery time is expected to be longer. At the end of rain event 1, the upper canopy site did appear constantly the coolest site for six hours the during atmospheric warming until the start of rain event 2. The moisture retention of the epiphytes is likely to retard the re-stratification of the profile during the day relative to forests devoid of outer canopy epiphytes. A more detailed analysis of a 5-month dataset should elaborate further on this aspect.

At night, the onset of cloud before the rain caused the sharp increase in nocturnal temperatures before rain event 1. This affect was also found in Amazonian forest (Fitzjarrald and Moore, 1990). The mist caused some temperature profile homogenisation. However, it is not until the rain event becomes intensive that true temperature profile homogenisation is achieved. At this point, it appears that radiative cooling on the forest floor is halted and the profile is completely homogenised. The duration of nocturnal homogenisation could not be estimated from this single event. In Amazonian forest, it was estimated that after nocturnal wind, the profile recovery required at least twice the length of the turbulent event (Fitzjarrald and Moore, 1990). Given the much cooler temperatures and the moisture retention of the canopy in montane forest, nocturnal recovery could be expected to be much longer.

5.4.4 Altitude

The effects of altitude can be seen in the data by the steep rate of

decline in temperature throughout the canopy even before sunset. In a premontane forest in Costa Rica at 870 m asl, Freiberg (1997) observed a slow decrease in canopy temperature above and below the canopy until midnight. In the present dataset, temperature declines are steepest around sunset when air temperatures plummet until around 7:30 pm before slightly levelling off. Sharp temperature declines are characteristic of high elevation areas (Benisten *et al.*, 1997). The very constant saturated conditions are also characteristic of high altitude tropical cloud forests (Bruijnzeel and Proctor, 1995; Bruijnzeel and Veneklaas, 1998; Stadtmüller, 1987).

5.5 Conclusion

The findings in this chapter will have a significant effect on forest microclimatic theory. The results highlight the influence of epiphyte communities, canopy structure and turbulent events on the microclimatology of the montane forest ecosystem. The effects of the concentration of epiphytes in the outer canopy are summarised as follows. 1. A blanket of moisture is created at the top of the canopy that ameliorates day and night temperatures through evaporation and heat retention respectively. 2. The outer canopy layer is drastically thickened that improves the retention of long-wave radiation from the understorey directly below the canopy surface and increases shading just below the canopy surface. The effects of a heterogeneous canopy structure are summarised as follows. 1. Turbulent mixing is increased, which reduces the retention of long-wave radiation, increases exposure and radiative cooling in the understorey, and increases the heterogeneity of microclimatic distribution. 2. Direct solar radiation at high zenith angles impacts on a larger proportion of the canopy when compared to a closed forest. 3. Surface roughness is increased, which prevents large scale canopy surface inversions, reduces the decoupling of canopy and atmospheric air masses, and increases cloud water capture by vegetation. Rain events homogenise canopy profiles, reduce temperatures and radiative cooling, and prolong the return to pre-turbulent profiles for substantial periods.

The results also present a different perspective on epiphyte habitats.

They suggest that on this wet season forest profile, the outer canopy is not the extremely harsh epiphyte habitat as it is commonly conceived to be in other forest types. Likewise, trunk habitats, which are commonly considered the most stable of epiphyte habitats, were shown to be subject to slightly greater daily fluctuations. The montane forest canopy structure creates a variety of microclimates both vertically and horizontally. This is likely to be a large factor in explaining why some montane forests defy traditional views on the decline of plant diversity with altitude.

Chapter 6 Community Dynamics

6.1 Aims

The objective of this chapter is to deduce the dynamic aspects of the establishment and succession of upper canopy epiphyte communities to complete the forth research aim.

4. Determine the dynamics of the epiphyte community

The succession of epiphyte communities appears to follow similar patterns in most moist tropical forests, where non-vascular epiphytes colonise bare branch surfaces (primary succession) (Kurschner and Parolly, 1998a; Nadkarni, 2000) and create a more suitable branch habitat for vascular epiphytes (Dudgeon, 1923). A large diversity of vascular epiphyte species and lifeforms colonise branches (Griffiths and Smith, 1983; Hietz *et al.*, 2002; Hietz and Briones, 1998). However, there have been few detailed accounts, and current thinking is based primarily on qualitative descriptions.

In the epiphyte studies to date, the distribution of successional communities has been said to follow the gradient of branch diameter from the outer canopy (initial stages) to the inner canopy (later stages) (Freiberg, 1996; Rudolph *et al.*, 1998). In the same studies, the large inner branches are home to the majority of epiphyte species and represented the later stages of succession. However, Freiberg (1996) found that in his inner zone, epiphyte communities represented both initial and later stages, due to some epiphyte slumping. In the *Ficus* host of the present study, the effects of epiphyte slumping is intensified within the inner zone (see Chapter 4). This signifies that branch diameter cannot be used to represent putative successional stages. Thus, in order to investigate the dynamics of the epiphyte community, an alternative to branch diameter was necessary for the purposes of classifying epiphyte clumps into successional categories.

The approach was to classify the epiphyte clumps according to the number of epiphyte species they contained. The Johansson Zones were also used to further separate these classifications. The first assumption of the

classification is that a greater number of species represents a temporal accumulation rather than spatial fusing. The second assumption is that high richness clumps have a higher abundance of individuals based upon the abundance/richness relationship previously identified (Chapter 3). The third assumption is that the transition from Johansson Zone 5 to Zone 4 represents a successional time series. The classification is coarse and does not account for clump fragmentation through slumping though this is explored in the analysis.

The present study aims to describe the initial and latter stages of vascular epiphyte succession in the upper canopy. The research aim will be achieved in two stages. Firstly, a qualitative description of the initial stage of primary succession will be presented to establish the conditions present for vascular epiphyte colonisation. Secondly, the succession of vascular epiphytes is investigated through a comparison of the floristics and habitat characteristics of epiphyte clumps at three stages of species richness in the upper canopy.

6.2 Methods

For a qualitative description of primary succession, a collection of general qualitative observations from the understorey of study site and the canopy of the *Ficus* host is presented. These observations were made by the author during the sampling period of the present study in 2003 – 2004, and during a previous visit to the study area in 2001 - 2002.

In order to investigate secondary succession, an analysis of species accumulation was performed independently within both Johansson Zones 4 and 5. The sample sizes from Zones 3 and 2 were insufficient for such analysis. The clumps were classified into the clump richness categories of low richness (1 spp to 4 spp), medium richness (5 spp to 9 spp) and high richness ($\geq$ 10 spp). The clumps included in the analysis (n = 521) were those that contained at least one individual of a species with a percentage frequency of $\geq$ 5% occurrence within all the upper canopy clumps (n = 526).

In order to investigate the floristic composition of the richness groups, a contingency table analysis using a Chi-Squared test was used to test for differences between richness groups within each Johansson Zone in expected abundance of species, lifeforms and taxonomic groups that showed a percentage frequency of $\geq$ 5% occurrence within the total number of upper canopy clumps. Species with $\leq$ 5% occurrence were grouped and included as 'other species'.

In order to investigate the habitat characteristics of the richness groups, a 1-way ANOVA test was used to test for differences in environmental habitat variables between richness groups within each Johansson Zone. Distributions of environmental habitat variables were displayed with boxplots created in Minitab (2000). The differences between zones in environmental habitat variables were addressed in Chapter 4 and are not addressed further.

In order to investigate the floristic similarity of richness groups, an analysis of similarity test (ANOSIM) was performed on the clump richness groups using DECODA (Minchin, 2001). The dissimilarity matrix for ANOSIM tests was created with a Bray-Curtis dissimilarity coefficient and probabilities were calculated with 1000 random permutations.

In order to investigate the community structure of the richness groups, dominance/diversity curves for each richness group were plotted to describe the distribution of species and were tested for goodness of fit to logarithmic models using SigmaPlot (SPSS Inc., 2001).

6.3 Results

6.3.1 Primary Succession

Within the understorey, bryophytes appeared to dominate bark surfaces. Trunks were often completely covered by bryophytes with occasional crustose and fruticose lichens, the exception being only the smoothest-barked species. During the study period, bryophytes colonised thin ropes and apparatus installed in the understorey. Many miniscule orchids in the genus of *Lepanthes* were also collected on bare bark from trunks.

Epiphytes fell from the canopy regularly. From the 1 km of trail used on a daily basis at the study site, dislodged epiphytes could usually be recovered daily for voucher specimens. Often after windy weather, up to 10 clumps could be retrieved without leaving the trail.

In the upper canopy, lichens are dominant on branch surfaces. Within the smooth barked *Ficus*, nearly all branch surfaces within the upper canopy not occupied by vascular epiphytes were occupied by crustose lichens. These were usually accompanied by foliose lichen in the inner canopy, and by foliose and fruticose lichens in the outer canopy (Figure 37). Fruticose and foliose lichens were scattered between the clumps of vascular epiphytes, whose root bound humus was covered by associations of bryophytes. Branch tips were dominated by fruticose, foliose, and some crustose, lichens.

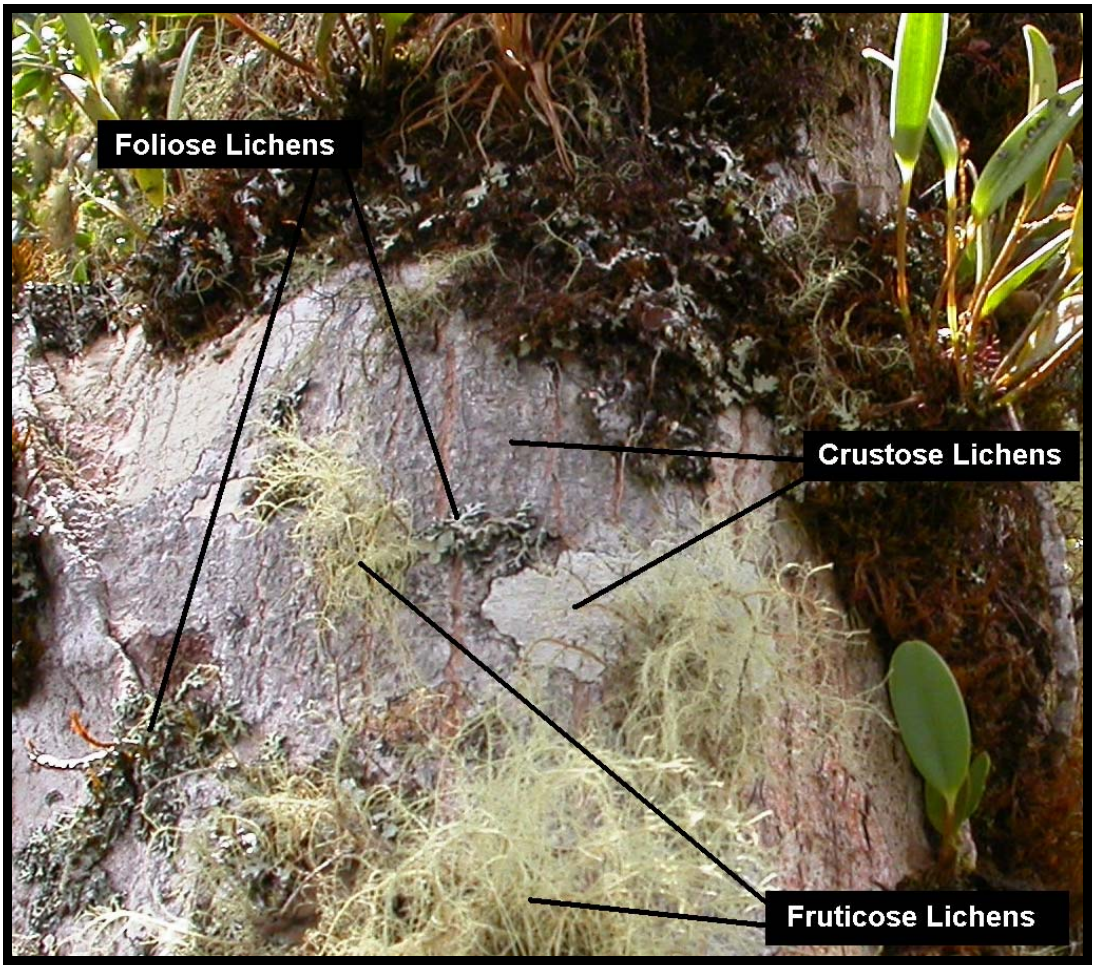


Figure 37: Crustose, foliose and fruticose lichens on branch surfaces of a *Ficus* host.

6.3.2 Vascular Epiphyte Succession

6.3.2.1 Environmental Habitat Variables

In Zone 5, RadMorn was significantly higher in the high richness group than any other group (Table 14). No other environmental habitat variables were significantly different among richness groups. Although non-significantly distributed, lower values of VisSky, TotBe and RadMidd were less frequent in the high richness group (Figure 39).

There was slightly higher heterogeneity in environmental habitat characteristics in Zone 4 than in Zone 5. LAIDev was significantly higher in the low richness group than the others while RadMidd was significantly lower in the low richness group than the others (Table 14). Again, the high richness group appeared to have a low frequency of low PAR and VisSky values. Though non-significant, the distribution of branch diameter shows how the high richness group is absent from large diameter branches in Zone 4.

6.3.2.2 Floristics

Nine types of Percentage Abundance (PA) trends were observed throughout the data. For clarity of interpretation, these trends are shown in Figure 38, and will be used as terminology throughout the results and discussion. Descriptive names relative to increasing richness have been used for each trend for ease of discussion but are not meant to imply any link between succession and increasing diversity. Skewed distributions were found in both directions and are prefixed by their direction of skew (eg. in Figure 38, all skewed trends displayed are decreasing). Only significant trends are reported and discussed.

Seventy-five percent of common species showed no difference in PA between Zone 5 richness groups, 61% showed no differences within Zone 4, and 53% showed no differences within both zones (Table 14). As shown above, clump abundance and richness are positively related (Figure 12).

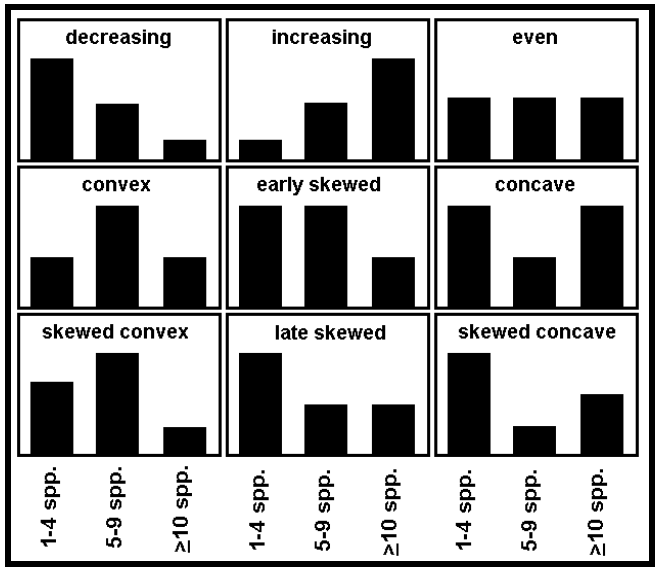


Figure 38: Percentage abundance trends relative to increasing clump richness.

Zone 5

In Zone 5, 53% of individuals were found in the medium richness group, 37% in the high richness group and 10% in the low richness group (Table 14). The medium and high richness groups contained the same number of species despite the difference in the richness of their clumps.

The long repent lifeform was the most abundant in the low richness group and had a decreasing trend. The open tank lifeform was the second most abundant lifeform and showed an even trend. The short repent lifeform displayed a decreasing skewed convex trend. The caespitose lifeform shows a strong increasing trend. The orchid group is the most abundant and shows a decreasing trend. Bromeliads, herbs and woody dicots all showed an even trend. The pleurothallid and fern groups show a strong increasing trend.

Maxillaria notylioglossa was by far the most abundant taxon and was the only species with a decreasing trend. *Maxillaria* sp. 1 and *Stelis campanulifera* both displayed a decreasing skewed convex trend. *Elaphoglossum* sp. 7 was unusually distributed with a concave trend. Three pleurothallid species, *Barbosella cucullata*, *Pleurothallis* sp. 19 and *P.* aff. *angustilabia*, all showed increasing trends. The increasing trend was also shown by the 'other species' group.

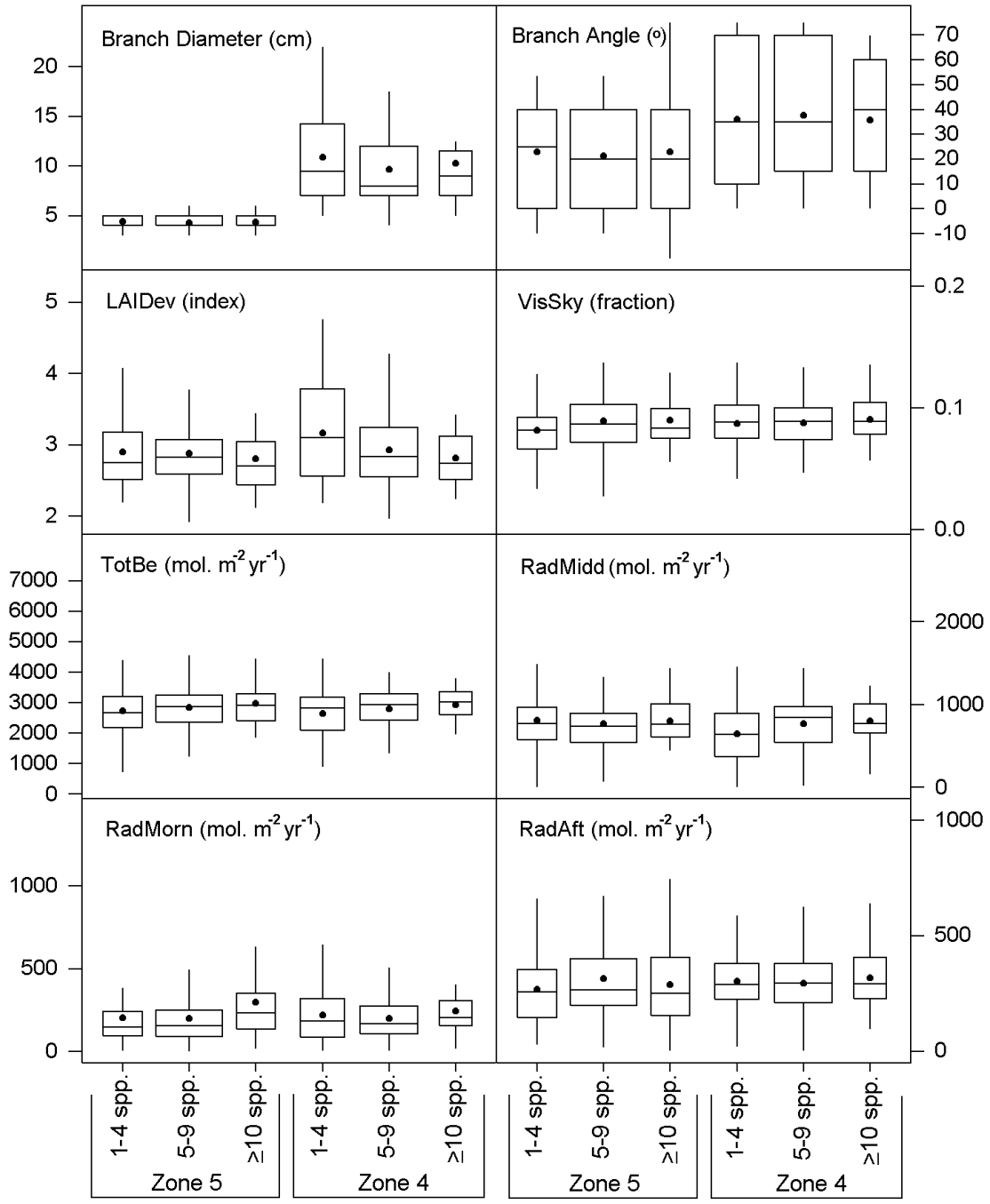


Figure 39: Boxplots of environmental variables within clump richness groups of Johansson Zones. Boxes represent the 2nd and 3rd quartile separated by the median line. Whiskers extend to the lower limits of the 1st quartile and the upper limits of the 4th quartile. Closed circles represent the mean and box width is relative to sample size.

Table 14: The means of environmental habitat variables and Percentage Abundance (PA) of lifeforms, taxonomic classes and common species within clump richness groups. Results of significance tests for abundances relate to a contingency table analysis of real abundance values.

Richness Group	low	medium	high		low	medium	high	
Zone	**5**	**5**	**5**		**4**	**4**	**4**	
Number of Clumps	**57**	**167**	**57**		**74**	**125**	**41**	
Species Richness (# spp.)	**39**	**85**	**85**		**56**	**85**	**87**	
Abundance (# individuals)	**444**	**2454**	**1760**		**445**	**1640**	**1046**	
Branch Diameter (cm)	4.40	4.31	4.35	NS	10.88	9.70	10.29	NS
Branch Angle	22.9	21.4	22.9	NS	36.0	37.8	35.9	NS
LAIDev (index)	2.90	2.88	2.81	NS	3.17	2.93	2.82	**
VisSky (fraction)	0.082	0.089	0.090	NS	0.087	0.088	0.091	NS
TotBe mol (mol.m-2/yr)	2736	2837	2984	NS	2655	2797	2943	NS
RadMidd (mol.m2/year)	807	770	801	NS	647	772	798	*
RadMorn (mol.m2/year)	205	199	299	**	220	199	244	NS
RadAft (mol.m2/year)	268	314	289	NS	303	294	317	NS
Ascending	**3.2**	**3.9**	**4.4**	**NS**	**3.6**	**6.2**	**7.6**	*
Caespitose	**5.6**	**13.7**	**23.2**	***	**8.3**	**22**	**26.9**	***
Lepanthid	**1.1**	**0.8**	**0.8**	**NS**	**7.2**	**1.6**	**0**	***
Long Creeping	**0.2**	**1**	**1.2**	**NS**	**15.7**	**5.4**	**7.9**	***
Long Repent	**49.5**	**35.3**	**26.4**	***	**12.4**	**11.9**	**14.1**	**NS**
Open Tank	**24.3**	**24.5**	**27.7**	**NS**	**31**	**28.3**	**23.6**	**
Pendant	**0.2**	**0.6**	**0.4**	**NS**	**0.4**	**1**	**1.2**	**NS**
Short Creeping	**9**	**9.6**	**10.9**	**NS**	**5.4**	**9.8**	**11.5**	**
Short Repent	**6.3**	**9.7**	**4.7**	***	**15.3**	**13.2**	**6.5**	***
Bromeliad	**24.8**	**25**	**27.8**	**NS**	**31**	**29**	**23.9**	**
Herb	**1.1**	**1.1**	**0.7**	**NS**	**0.9**	**1.8**	**2.3**	**NS**
Orchid	**51.6**	**39.9**	**31.1**	***	**15.7**	**15.7**	**20.5**	**
Pleurothallid	**11.5**	**20.9**	**24.1**	***	**26.7**	**31**	**27.2**	**NS**
Fern	**7.9**	**9.3**	**11.3**	*	**21.3**	**15.7**	**19.3**	**
Woody Dicot	**3.2**	**3.7**	**5**	**NS**	**4.3**	**6.7**	**6.8**	**NS**
Barbosella cucullata	**0.5**	**2.4**	**3**	**	**0.7**	**3.3**	**4.7**	***
Bromeliaceae sp 01	**7.9**	**6.3**	**7.3**	**NS**	**9.7**	**7**	**6.4**	**NS**
Bromeliaceae sp 02	**12.6**	**13.3**	**15.3**	**NS**	**20.2**	**19**	**15.6**	*
Bromeliaceae sp 03	**2.3**	**3.4**	**3**	**NS**	**0.7**	**0.9**	**0.6**	**NS**
Bromeliaceae sp 04	**0.2**	**0.7**	**0.7**	**NS**	**0.2**	**1.3**	**0.1**	**NS**
***Disterigma* sp 01**	**1.6**	**1.1**	**1.4**	**NS**	**0.9**	**1.1**	**1.7**	**NS**
Elaphoglossum latifolium	**0.2**	**0.3**	**0.1**	**NS**	**4.9**	**2**	**3.6**	**
***Elaphoglossum* sp 01**	**0.2**	**0.6**	**1**	**NS**	**0.2**	**1.4**	**1**	**NS**
***Elaphoglossum* sp 02**	**0**	**0.4**	**0.3**	**NS**	**3.6**	**2**	**2.8**	**NS**
***Elaphoglossum* sp 07**	**5.4**	**3.5**	**5**	*	**2**	**4.6**	**4.2**	**NS**
***Elaphoglossum* sp 09**	**0**	**0.3**	**0.7**	**NS**	**2.7**	**1.2**	**1**	*
***Elleanthus* sp 01**	**0.2**	**0.8**	**1.2**	**NS**	**3.1**	**3.2**	**2.7**	**NS**
***Epidendrum* sp 03**	**1.4**	**2.4**	**2.3**	**NS**	**0**	**1.3**	**2**	**
***Lellingeria* sp 01**	**1.1**	**2.6**	**2.6**	**NS**	**1.3**	**2.2**	**2.6**	**NS**
***Masdevallia* sp 01**	**1.1**	**2.4**	**3**	**NS**	**0.4**	**4.1**	**3.1**	**
Maxillaria notylioglossa	**40.5**	**22.5**	**16.6**	***	**7.6**	**4.9**	**8**	**
***Maxillaria* sp 01**	**8.1**	**10.4**	**6.5**	***	**0.4**	**1.8**	**1.7**	**NS**
***Maxillaria* sp 13**	**1.4**	**1.6**	**0.9**	**NS**	**0.7**	**0.2**	**0.5**	**NS**
***Melpomene* sp 01**	**0.5**	**0.6**	**0.6**	**NS**	**0.7**	**0.9**	**1.2**	**NS**
***Peperomia* sp 01**	**1.1**	**1.1**	**0.6**	**NS**	**0.9**	**1.5**	**1.9**	**NS**
Pleurothallis* aff. *angustilabia	**0**	**1.3**	**2**	**	**0.2**	**1.6**	**2.2**	*
Pleurothallis matudina	**0.2**	**0.2**	**0.7**	**NS**	**1.1**	**1.8**	**3.8**	**
***Pleurothallis* sp 11**	**1.4**	**3.1**	**2.4**	**NS**	**4.7**	**5.1**	**3.2**	**NS**
***Pleurothallis* sp 19**	**0.9**	**1.4**	**6.8**	***	**0.2**	**1.8**	**3.8**	***
Prosthechea fusca	**0**	**0.5**	**1.3**	**NS**	**0.4**	**0.6**	**0.8**	**NS**
***Scaphyglottis* sp 01**	**0**	**0.5**	**0.3**	**NS**	**0.4**	**0.9**	**0.6**	**NS**
***Sphyrospermum* sp 01**	**0.9**	**1.8**	**2.3**	**NS**	**3.1**	**3.8**	**3.3**	**NS**
Stelis campanulifera	**5**	**6.5**	**2.2**	***	**10.6**	**7.4**	**3.2**	***
Other spp.	**5.4**	**8.1**	**9.7**	**	**18**	**13.1**	**14**	*

Environmental Variables: 1 - way ANOVA
Abundance Variables: Chi-Squared test

NS : no significant differences
*** : P < 0.05**
**** : P < 0.001**
***** : P < 0.0001**

Zone 4

Many of the trends found in Zone 5 are repeated through Zone 4. Fifty-three percent of individuals were found in the medium richness group, 33% in the high richness group and 14% in the low richness group. The medium and high richness groups again had a similar number of species. The ascending, caespitose and short creeping lifeforms all show an increasing trend. The lepanthid lifeform shows a strong decreasing late skewed trend, both the open tank and short repent lifeforms show a decreasing early skewed trend and the long creeping lifeform shows an unusual decreasing skewed concave trend. The open tank lifeform is the most abundant in all richness groups. The bromeliads show a decreasing early skewed trend, the ferns showed an unusual concave trend and the orchids show an increasing late skewed trend that for the latter is a reversal compared to Zone 5. The pleurothallids are the most abundant in every richness group but show an even trend.

Barbosella cucullata, *Epidendrum* sp. 3, *Pleurothallis* sp. 19, *P. matudina* and *P.* aff. *angustilabia*, all show increasing trends. *Masdevallia* sp. 1 shows an increasing skewed convex trend. *Maxillaria notylioglossa* and *Elaphoglossum latifolium* were both unusually distributed with a concave trend. Despite the reduction in abundance in Zone 4, *M. notylioglossa* is still the third most abundant taxon. The 'other species' show a reversal in Zone 4 with a decreasing late skewed trend and Bromeliaceae sp. 2 shows a decreasing early skewed trend. The latter is also the most abundant species in all richness groups. *Elaphoglossum*. sp. 9 and *Stelis campanulifera* both show a decreasing trend in Zone 4.

Similarity

In Zone 5, the greatest similarity in Zone 5 was between the medium and high richness groups (Table 15). In Zone 4, the high richness group was very similar to both the other groups. Between zones, the highest similarity between groups was the Zone 5 high richness group and the Zone 4 medium richness group. The most dissimilar groups were the Zone 5 medium richness group and the Zone 4 low richness group.

Table 15: ANOSIM results for clump richness groups. 1 = Zone 5 low richness, 2 = Zone 5 medium richness, 3 = Zone 5 high richness, 4 = Zone 4 low richness, 5 = Zone 4 medium richness, 6 = Zone 4 high richness. Community average R = 0.19, *P* = < 0.0001.

	1	*prob*	**2**	*prob*	**3**	*prob*	**4**	*prob*	**5**	*prob*
2	0.150	*0.000*								
3	0.258	*0.000*	0.006	*0.564*						
4	0.085	*0.000*	0.444	*0.000*	0.148	*0.000*				
5	0.206	*0.000*	0.217	*0.000*	0.025	*0.169*	0.182	*0.000*		
6	0.274	*0.000*	0.215	*0.000*	0.224	*0.000*	0.064	*0.996*	0.099	*0.998*

6.3.3 Community Structure

The dominance/diversity curves of each richness group were best fitted to lognormal distributions (Figure 40), as seen in the previous analyses. The Zone 5 medium richness group had the best fit, while the Zone 4 medium richness group showed the worst. Once again, as seen in the Johansson Zones and the single tree, the frequency of the rarest species is much higher than typically predicted by lognormal distributions. The curve for the Zone 5 low richness group appeared distorted. This suggests the presence of a second guild of species.

6.4 Discussion

6.4.1 Primary Succession

The patterns of non-vascular epiphyte distribution found in the upper canopy of *Ficus* hosts, conform to those reported from other moist montane forests (Dudgeon, 1923; Hietz, 1997; Nadkarni, 2000). This change of dominance from bryophytes to lichens from the lower to upper canopy is likely to be a result of the difference in disturbance, radiation and drying regimes. In the upper canopy, only a few patches of bryophytes were devoid of vascular species. This supports the notion that early vascular colonisers may be equally important in community succession as bryophytes. Dudgeon (1923), from the Himalayas, observed that ferns and other vascular epiphytes colonised bryophytes at the very last stage of succession. However, his

area lacked the prolific pleurothallid orchids (*Lepanthes, Lepanthopsis*, *Trichosalpinx*) of the neotropics, which can colonise exposed substrates (Tremblay, 1997). Nevertheless, lichens and bryophytes provide the building blocks for the development of tropical montane vascular epiphyte communities. The majority of vascular species appeared to require these important colonising species in order to provide a rooting and anchoring substrate.

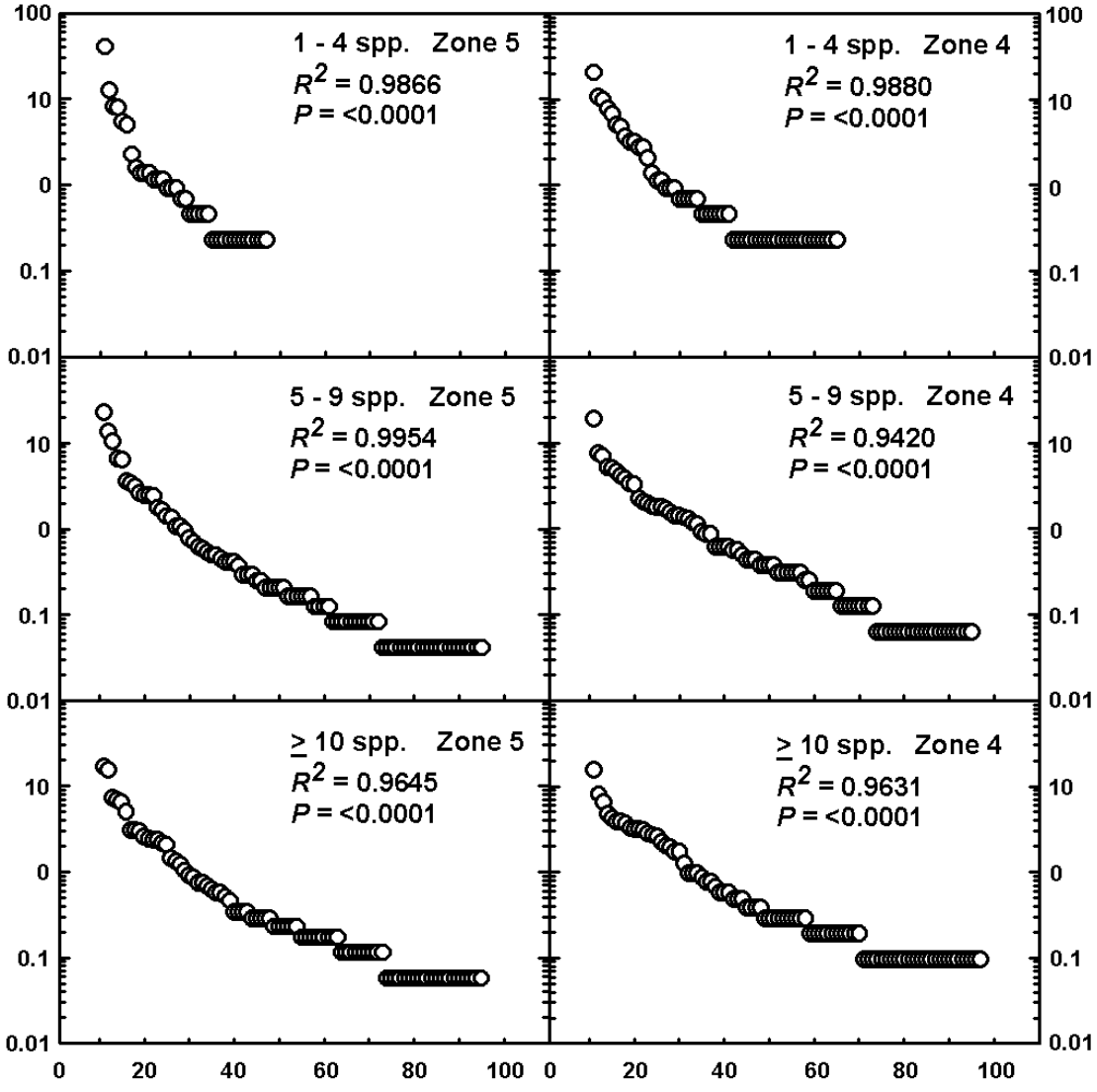


Figure 40: Dominance/diversity plots fitted to a lognormal model for each clump richness group. Percentage abundance on a log scale (Y) of all epiphyte species in rank order of abundance (X).

6.4.2 Vascular Epiphyte Succession

6.4.2.1 Environmental Habitat Variables

There were few significant differences in environmental habitat variables between clump richness groups within zones compared to the differences observed between zones. This indicates that clump richness is well mixed throughout the environments present in both the zones. However, despite the even distribution of branch diameter within zones, high clump richness appears to be related to higher PAR. In Zone 5, the highest richness was associated with a higher RadMorn. As previously demonstrated (Chapter 4), epiphytes in Zone 5 are located where PAR receipt is far from the expected maxima of the outer canopy. Whilst epiphytes select shaded habitats, the higher RadMorn, indicates that the higher richness group is that located near the periphery of the canopy where radiation receipt at high zenith angles is relatively high. This could be supported also by the wider range of branch angles that is a feature of the outer most zone.

In Zone 4, the low richness group was associated with low RadMidd and high LAIDev (increased branch shading), which also supports a notion of the positive relationship between PAR and clump richness. The low richness group was found to comprise of a larger proportion of clumps from larger branch diameters. This is likely to have influenced the high LAIDev.

6.4.2.2 Zone 5

In Zone 5, the notion that the low richness group represents a colonising group is supported by a number of floristic elements. In the analysis of floristic similarity, the low richness group was the most dissimilar to any other group. In contrast, the medium and high richness groups were shown to be very similar.

The dominance/diversity curve of the low richness group appeared to have a distortion akin to a broken-stick distribution as seen by the relative increase in the frequency of low abundance species along the curve. Wilson (1993) describes why broken-stick communities are rarely detected in lognormal distributions. Regardless, the curve is suggestive of a second

guild of species. This suggests that the group is represented by both colonising clumps, and, clumps representing later successional communities.

In the low richness group, *Maxillaria notylioglossa,* the dominant taxa of the entire community, is vastly over-represented. Other than the absence of many common species, of note is the low PA of most *Elaphoglossum* species (not shown statistically) and ferns in general (except *E*. sp. 7, a hardy outer canopy specialist). The lower PA of ferns is suggestive of low moisture availability. The majority of fern species are intolerant of dry conditions and their distribution within the canopy has been correlated to moisture (Hietz and Briones, 1998).

Stelis campanulifera is the only pleurothallid orchid to follow a decreasing type trend in Zone 5, and is a canopy generalist. It had a high observed fecundity and a short repent lifeform. The decreasing skewed convex trend may be explained by its ability as a generalist to colonise new habitat, though lacking the outer canopy coloniser adaptations that would allow it to be a pioneer species. Pleurothallid species, the caespitose lifeforms and the pleurothallid group all showed increasing trends that highlight the preference of pleurothallids for the well developed clumps of high richness. Many pleurothallids rely on imbibing roots for both water and nutrient uptake (Benzing and Pridgeon, 1983). This may limit their ability to colonise in the early stages of clump development. In contrast, bromeliads, whose leaves and tanks (in tank species) are often of more importance than roots for moisture and nutrition (Adams and Martin, 1986; Benzing and Davidson, 1979; Benzing and Renfrow, 1974), are evenly distributed throughout all groups.

The convex trend for *Maxillaria* sp. 1 may reflect its lifeform. Whilst being similar by taxonomy and branch diameter distribution to *M. notylioglossa*, its short repent lifeform would restrict its spreading ability relative to the long repent form of *M. notylioglossa*. The caespitose lifeform is particularly poorly represented in low richness groups relative to its dominance throughout the zones, and the tree, that reflects its lack of vegetative colonising ability.

The dynamic nature (tree growth) of the colonisation front in the upper canopy appears to create a specialised niche that is completely dominated by *M. notylioglossa* and the bromeliads. *M. notylioglossa* has a long repent (spreading) habit well adapted to this location. Uncolonised humus deposits can be reached with running stolons without the need for reproductive success. These stolons were sometimes observed traversing bare branch substrates between a colonised and uncolonised clumps. All of the common bromeliads produce large quantities (when fertile, which is rarely) of wind dispersed plume seeds to overcome their lack of mobility. Orchid dust seeds offer potentially the best adaptation for carriage to and anchorage within humus deposits. However, thin branches were often bare, and, in the present study, were often solely occupied by fruticose lichens. The bromeliad plume seeds, often with hooked coma hairs (Benzing, 1990), may present the best method of anchorage within lichens on bare branches exposed to wind and rain. Similarly, the juvenile morphology of many bromeliad species allows independence from humus at establishment through the ability to collect water and nutrients through leaves (Adams and Martin, 1986).

The majority of species had a preference for thick humus deposits. Furthermore, while a few colonising species declined, there were no common colonising species that were absent from rich clumps. Some twig epiphytes collected from the outer zone were likely to be absent from humus deposits, though none of these species showed sufficient frequency to be included in the analysis.

6.4.2.3 Zone 4

Whilst the transition from low richness to high richness in Zone 5 probably represents community growth and the natural order of succession, in Zone 4, clump richness is less defining. There were PA distributions with concave trends, colonising species with high PA in the low richness group, and, a high floristic similarity between the low richness groups of both zones. Defining the Zone 4 low richness group is crucial to understanding the dynamic processes. Given that both the mean clump richness of Zone 5 was seven species (Table 8 – Chapter 4), and, that Zone 4 clumps are potentially

older, the Zone 4 low richness clumps could represent either of: 1). an exclusion of species from clumps in epiphyte succession; 2). a drop in species richness through the physical reduction of clump size (fragmentation) by slumping; 3). or, an early successional clump in the process of establishment upon space made available by slumping.

The most important step was to determine the natural successional order of the Zone 4 groups. This can be achieved by tracking the PA of the most abundant and colonising species *Maxillaria notylioglossa*. The Johansson Zone distribution of this species peaked in PA in Zone 5, and, despite its complete dominance in the upper canopy, it was one of the few species without a single individual in Zone 3 (Chapter 4). The latter highlights its suitability as a successional indicator species. Thus, the declining PA trend of this species is possibly the best indicator of the natural successional order.

What was found for *M. notylioglossa* was an unusual concave trend, which followed the tendency for a higher proportion of unusual concave PA trends in Zone 4 than was found in Zone 5 (21% vs. 7%). Concave trends defy explanation under a single successional ordering of richness groups.

The first clue to understanding the *M. notylioglossa* trend is its Zone 5 decreasing trend. The decline of PA along the successional order was 44% from the low richness group to the medium richness group and 26% from the medium richness group to the high richness group. It could be expected that the group to follow or adjoin the Zone 5 high richness group in the successional order would show a PA for *M. notylioglossa* reduced by the same order of magnitude as those previously. This was either the low richness group or the high richness group, either of which showed the decline of PA at the same order of magnitude as those previous (54% low, 70% medium, 51% high). The latter is the most logical choice as the next successional group, as evidenced by the similar species richness of the group (87 spp. - Table 14).

The decline in PA for *M. notylioglossa* continue at the same order of magnitude into the medium richness group. This is accepted as the natural order based on the very slight decline in species richness (85 spp. - Table 14).

Though this does not suggest that clumps decline in richness with age. As will be demonstrated, these older clumps, based on *M. notylioglossa* PA, represent the fragmentation of clumps through slumping over time. Such an explanation follows the general trends shown previously for the smaller size and frequency of clumps on larger branches that was believed to represent an increase in slumping probability with time.

The similarity of the species richness of the high and medium richness groups suggests that fragmentation causes the reduction in the size of the clump, which in turn reduces the richness based on the abundance/richness relationship. This suggestion is evidenced by the ANOSIM. The floristic similarity of the Zone 4 richness groups was marked and the floristic composition of the high and medium richness groups is practically identical. This suggests that the transition between high and medium richness groups cannot be associated with a significant turnover or loss of species. Thus, the species richness of medium and high richness groups within Zone 4 would appear to be related to the severity of fragmentation through slumping.

However, the higher PA of *M. notylioglossa* in the low richness group is not explained by this summation. Such a trend reversal in this colonising species can be explained by recolonisation. The process of slumping affects the size and longevity of existing clumps, but it also serves the function of providing space for recolonisation. Such recolonising clumps are undoubtedly of a younger age than undisturbed Zone 4 clumps, and thus, are likely to contain less species. It is suggested that a proportion of the low richness group is represented by recolonising clumps. This suggestion explains why the colonising *M. notylioglossa* shows a higher PA in what could only otherwise represent the oldest and most fragmented clumps. Thus, it is suggested that the low richness group represents a composite of recolonising clumps and older, more fragmented clumps.

This suggestion is also supported by ANOSIM tests. The floristic similarity between the low richness group and other groups is very high. In fact the similarity with the high richness group is marked. This suggests that fragmentation continues to occur without a significant loss or turnover of

species. An explanation of Zone 4 low richness clumps via other means than non-fragmentation implies a species drop out or turnover that would result in a low floristic similarity with the other groups. Furthermore, the colonising Zone 5 low richness group shares its highest floristic similarity with the Zone 4 low richness group that suggests the presence of similar colonising species. The difference in the above-mentioned pairwise ANOSIM results, suggest that the proportion of colonising clumps in the low richness group is lower than the fragmented clumps.

Possibly the strongest floristic evidence for the presence of recolonising clumps is the strong decreasing trend of the lepanthid orchids. Though not represented by a single common species, this diverse group (3 genera, 16 spp.) has markedly higher PA in the Zone 4 low richness group than all other groups. Lepanthid orchids are very small plants that typically flower successively year round (Luer, 1996; Tremblay *et al.*, 1998). Their ability to colonise bare bark is well known and was also reported statistically by Catling and Lefkovitch (1989) in Guatemala. These species were also common on the bare bark of trunks in the understorey (above) and were progressively more abundant in the lower Johannson Zones (Table 8 - Chapter 4). The latter highlights its preference for uncolonised bark and shade as a coloniser in shaded environments (Catling and Lefkovitch, 1989). In the canopy, the species were sparsely distributed as found in other work (Tremblay, 1997). The lepanthid role as a bark coloniser makes the possibility of an association with the oldest epiphyte clumps of Zone 4 highly unlikely. Thus, the abundance of lepanthid orchids in the low richness group is further evidence of recolonising clumps.

6.4.2.4 Inner Canopy Recolonisation

With such a dense and diverse outer canopy flora, and the larger surface area for establishment of the inner canopy, the question that arises is why inner canopy recolonisation does not occur at the order of magnitude seen in the outer canopy. The process of recolonisation on large inner canopy branches must be considerably different to colonisation in the outer canopy.

The recolonisation of large branch surfaces appears to take longer than colonisation at the branch tips (Nadkarni, 2000). Large bare surfaces offering little surface roughness are expected to increase the difficulty of attachment for colonisers (Nadkarni, 2000) through the typical means of branch encirclement by roots (Chase, 1987).

The grow rates of many epiphytes is slow (Zotz, 1995), due to the low availability of nutrients available in the canopy (Benzing, 1990). However, some species with colonising roles have been shown to exhibit (by necessity) high growth rates (Curtis, 1952; Hietz *et al.*, 2002; Richardson *et al.*, 2000). Furthermore, establishment in the canopy for most species is related to high energy expenditure through high growth rates relative to later life stages (Hietz *et al.*, 2002) This need for relatively high energy expenditure may also explain the high mortality of juveniles found in many studies (Benzing, 1981; Hietz, 1997; Hietz *et al.*, 2002; Larson, 1992).

It could be expected that colonising species in the outer canopy of montane cloud forests receive a higher amount of much needed metabolic assistance in the outer canopy than other canopy zones. There, the rate of potential PAR is high and accessibility to moisture from passing mists is highest due to the diffusion of flow within the canopy (Kowalski and Vong, 1999), which may be exacerbated in the present context due to the outer canopy thickening with high epiphytic growth (Chapter 4). Thus, inside the canopy, establishing epiphytes would be significantly disadvantaged by the lower PAR, lower accessibility to moisture from passing mists (though less evaporation), and a larger metabolic expenditure for root growth in order to secure an attachment on the larger surface area. Hietz (1997) also found that some bromeliads had a higher mortality on larger branches, that he attributed to poor photosynthetic efficiency. Furthermore, in the host of the present study, increased branch angle and cooler night and day temperatures associated with the inner canopy may contribute further to poor establishment conditions.

The low RadMidd and high LAIDev demonstrate the higher shading of the low richness groups relative to other groups. The distribution of branch

diameters also demonstrates how the low richness group is relatively better represented toward the inner crown. The two prolific bromeliad species are better represented in the low richness group than in all others, where they are also abundant. This could be explained by a high photosynthetic efficiency under low light conditions, a common feature of mesic tank bromeliads with sparse trichome cover (Benzing and Renfrow, 1971; Griffiths *et al.*, 1984). *Stelis campanulifera* is the other prominent species that is a prolific generalist in all zones of the canopy from the outer branch tips to shaded trunks of the understorey. It appears to favour low richness clumps in all zones.

6.4.2.5 Bromeliad Microhabitats

One other anomaly emerged from the Zone 4 analysis. Recolonisation did not explain the concave and decreasing trends of the fern species, the long creeping fern lifeform and the fern group. Generally, ferns would be expected to prefer the higher moisture offered by well-developed clumps as seen in zone 5. These concave abundances can be explained by the occurrence of a special microhabitat. The microhabitat is formed at the attachment of large mature tank bromeliads (sp. 1 and 2). These attachments providing a secure rooting, shading and watering opportunity beneath the large rosette. Yet, the size of the habitat restricts the number of individuals, and thus the richness is low or medium.

The tank bromeliad attachments housed a variety of epiphytes, but predominantly favoured fern and orchid species (Table 16). These microhabitats provide habitat more similar to a large established, and in the present context, species rich epiphyte clumps, where moisture and temperature fluctuations are lower (Freiberg, 2001; Stuntz *et al.*, 2002), and nutrient availability is higher (Bohlman *et al.*, 1995; Ingram and Nadkarni, 1993) relative to uncolonised branches or thin humus deposits. In fact, the larger bromeliads slowly leak water withheld in their tanks for long periods after rain and the humus surrounding the attachments may be completely saturated whilst all other deposits are dry (pers. obs.). Thus, the species present in these microhabitats, are also species that prefer the protection of a large clump.

Table 16: Percentage abundances within clumps on the attachments of bromeliads

Richness Group	1-4 spp.	5-9 spp.	1-4 spp.	5-9 spp.
Zone	5	5	4	4
Number of Clumps	1	3	7	9
Abundance (# individuals)	9	46	28	52
Orchids (16 spp.)	44.4	52.2	14.3	59.6
Ferns (13 spp.)	55.6	41.3	71.4	25.0
Other (5 spp.)	0.0	6.5	14.3	13.5

Pleurothallis matudina is one of the most morphologically variable and widely distributed pleurothallid orchids within the study area, and more generally, the neotropics. The largest encountered specimens of this species were those found growing on bromeliad attachments. This suggests that bromeliads provide one of the least limiting epiphyte habitats. Many ferns and an unidentified dicotyledonous angiosperm were restricted to these bromeliad attachments (*Cochlidium* sp. 1, *Lellingeria* sp. 2, *Lellingeria subsessilis*, *Pecluma* sp. 2, Dicotyledonae sp. 5).

6.4.2.6 Successional Order

In an ombroplilous forest, Freiberg (1996) found that the latter stages of succession housed more species, but that there was a turnover from the outer canopy to the inner. Furthermore, the patterns he observed were linked to humus accumulations with deeper humus having more species. However, in a montane forest, Rudolph *et al.* (1998) found that species richness remained the same on older and younger branches, but there was a species turnover. They also found that older branches had fewer individuals of a larger size than younger ones. These results highlight the effect of slumping in the host of the present study. Whilst similar patterns may exist within other hosts of the forest, in the *Ficus*, it is unclear whether a late successional community could exist. However, both these studies found a larger number of specialist colonists that were not present in later communities. The present analysis could not reveal evidence of broad scale species turnover within common species. However, rare species, some of which were undoubtedly linked to either twigs or deep humus, could not be included in the statistical tests.

The lack of relay succession was a distinctive feature of the results. This is exemplified in the distribution of the most common colonising species. Whilst *M. notylioglossa* declined in PA along the successional order, it remained one the most abundant species in all richness groups. The strategies of tank bromeliad species epitomise the flexibility of canopy epiphytes. Many species are dimorphic, displaying juvenile (atmospheric) and adult (tank) morphologies (Adams and Martin, 1986). The outer canopy can be colonised with imbibing and desiccation tolerant leaves (atmospheric) in the absence of nutrient and moisture reserves. As the plant increases in size and resource requirements, the leaf structure changes to form the water-impounding tank (Adams and Martin, 1986).

6.5 Conclusion

Epiphyte slumping is common on the inclined and wide branches of Zone 4. This results in the presence of clumps that have never slumped from branches (late successional), clumps that have been fragmented by partial slumping, and clumps that recolonised the ample bare space created by slumping (early successional). None of these successional stages can be clearly distinguished by either clump richness or branch diameter categories. The efficiency of epiphyte slumping reduces the proportional representation of undisturbed late successional communities. No evidence of large-scale relay succession was found, possibly as a consequence of this slumping.

The explanation for the immense species richness of the *Ficus* host appears to be related to epiphyte slumping. The present analysis suggests that the period between colonisation and a species rich community is relatively short, and, that the floristic similarity between clumps of differing species richness is high. The ample space provided by slumping within the inner canopy appears difficult to recolonise.

Chapter 7 Species Distributions and Associations

7.1 Aims

The objective of this chapter is to critically analyse the patterns of species abundance, and to determine the species associations, the overlap of species ranges and the ecological relationships within the upper canopy epiphyte community in order to complete the fifth research aim.

5. Determine the ecological mechanisms influencing the species distribution and association in the upper canopy

The abundance of species within communities and the mechanisms influencing distributions have been well studied in many ecosystems, but not in epiphyte communities in tropical montane cloud forests. Some authors have addressed species distributions (Bennett, 1986), guilds (Kernan and Fowler, 1995) and coexistence (Benzing, 1981) in epiphyte communities, though these are predominantly from simple and species poor communities found in less humid ecosystems. Hietz and Hietz-Seifert (1995b) and Hietz (1997; 1995a) present the most detailed account of population dynamics and community structure in a montane epiphyte community to date. However, their Mexican community is considerably less species rich than that studied herein, the study area has a lower altitude and the principal phorophytes are fissured-bark and deciduous oaks.

The research aim will be achieved by a number of means. To describe the distribution and the influencing mechanisms on the abundance of species, the dominance/diversity curve will be critically analysed, and the establishment strategies of the resident epiphytes will be discussed. Multivariate analyses will be used to describe the species associations and ecological relationships within the clump arrangements of the upper canopy. The amount of overlap in the area occupied by epiphyte species within the upper canopy clumps will be investigated with pairwise species comparisons.

7.2 Methods

Only clumps that contained at least one individual of a species with a percentage frequency of ≥ 5% occurrence within the clumps of Johansson Zones 4 and 5 (common species) were used in all analyses (n = 521).

7.2.1 Community Structure

In order to describe the distribution of species in the upper canopy community, a dominance/diversity curve was tested for goodness of fit to logarithmic models using SigmaPlot (SPSS Inc., 2001).

7.2.2 Life Strategies

In order to describe the life strategies of the common species in relation to their canopy roles, the seed type, flowering phenology, and the population fertility rate were noted for each common species. The Population Fertility Rate (F') is the percentage of clump populations with a flowering/fertile[2] individual during each flowering period. The F' was estimated by determining both the percentage of flowering/fertile specimens for each common species recovered from grow house collections, and, the percentage of clump populations with flowering/fertile individuals for each common species during the relevant flowering periods. The grow house appeared to be a suitable environment for the canopy species with a 98.5% survivorship over the course of the study. Grow house specimens received rainwater passively and at the same rate as the canopy, though they received less mist. In dry periods, extra watering from collected rainwater was applied to encourage flowering. In every case when grow house species were subsequently encountered in the canopy during their respective flowering period, the percentages of the *in situ* populations was mimicked in the grow house and the percentages.

For the few common species for which no fertile individuals could be found (Bromeliaceae sp. 3, Bromeliaceae sp. 4, *Epidendrum* sp. 3, *Elleanthus*

[2] In the present chapter, flowering relates to angiosperms bearing a flower and fertile relates to pteridophytes bearing a fertile leaf. Fruiting is not investigated in the present study.

sp. 1, *Masdevallia* sp. 1), F' was estimated from the proportion of recorded individuals in the population that bore fruit from the previous season during the period when fruits were present. Thus, the fertility rates shown here are a crude estimate that nonetheless shows differences between species.

In order to describe the importance of F' for the epiphyte community inclusive of seasonal effects, the probability of finding flowering/fertile individuals of each common species in any clump at any time during the respective flowering period (P'_{period}) was calculated as:

$$\mathbf{P'_{period} = (F' \times PF) / D'}$$

where F' = fertility rate (percentage) and PF = percentage frequency of species within clumps (fraction). D' = duration of flowering/fertility period (months).

In order to determine the proportion of species flowering/fertile within clumps for each month of the year, a total of P'_{period} for each month was calculated by summing the P' time of each species that was flowering/fertile for each month.

7.2.3 Species Associations

In order to investigate epiphyte species associations, a floristic classification was performed using a hierarchical cluster analysis of the selected upper canopy clumps. The cluster analysis was performed using PC-ORD (McCune and Mefford, 1999) with a reduced binary dataset that only included the 28 common species. The cluster analysis used the Ward's Method and a Euclidean (Pythagorean) distance measure to produce a dendrogram scaled by Wishart's (1969) objective function.

In order to investigate the ecological significance of the cluster analysis groupings, a 1-way ANOVA test was used to test for differences between cluster groups in clump and environmental habitat variables. The distributions of clump and environmental habitat variables within and between cluster groups was displayed with boxplots created in Minitab (2000). Clump variables include abundance per clump (# of individuals), richness per clump

(# of species) and ‘other species' per clump (% of total richness of species with ≤ 5% occurrence in upper canopy clumps).

In order to investigate the significance of the floristic associations of the cluster analysis groupings, a contingency table analysis using a Chi-Squared test was used to test for differences in the frequency of occurrence between cluster groups of common species. The differences in proportion of Johansson Zone 4 and 5 between cluster groups was also tested with this method. In order to investigate the floristic similarity of the cluster analysis groupings, an analysis of similarity test (ANOSIM) on the cluster groups was performed using DECODA (Minchin, 2001). The dissimilarity matrix for ANOSIM tests was created with a Bray-Curtis dissimilarity coefficient and probabilities were calculated with 1000 random permutations.

In order to investigate the relationship between all environmental habitat variables and the floristic composition, a floristic ordination was performed using Non-linear Multidimensional Scaling (NMS). The NMS ordinations were performed using PC-ORD (McCune and Mefford, 1999) with a reduced dataset that only included the 28 common species. Cluster analysis grouping scores were included with environmental habitat variables. The ordination technique used the method developed by Mather (1976) and Kruskal (1964) with a Bray-Curtis distance matrix. The ordination was run forty times from a random starting configuration with the real data and dimensionality was assessed with a Monte Carlo test with fifty runs of randomised data. DECODA (Minchin, 2001) was used for vector fitting of maximum correlation values of environmental habitat variables to the NMS ordination axis. The significance of the maximum correlation values was tested using 1000 permutations from a random starting configuration.

In order to quantify the overlap of species distributions within the upper canopy, a niche overlap analysis was performed on the upper canopy clumps using EcoSim (Gotelli and Entsminger, 2001). The niche overlap analysis was performed using the pairwise and symmetric Pianka’s (1973) Index.

The Pianka's Overlap Index for species 1 and 2 (O'_{12}), with niche area utilisations P_{1i} and P_{2i}, is calculated as:

$$O'_{12} = O'_{21} = \frac{\sum_{i=1}^{n} P_{2i} P_{1i}}{\sqrt{\sum_{i=1}^{n} (P_{2i}^{2})(P_{1i}^{2})}}$$

The analysis used a reduced binary dataset that only included the 28 common species. The randomisation algorithm used was that of Winemiller and Pianka (1990) with niche breadth retained and zero states reshuffled. The distribution of resource states was treated by the equiprobable assumption. The null model was calculated with 1000 random permutations. Niche overlap (O') is reported as: 0 = no overlap and 1 = complete overlap. In order to determine the effect of percentage frequency within clumps on the mean O' of each common species, a Pearson correlation test was performed.

7.3 Results

7.3.1 Community Structure

The dominance/diversity curve follows a lognormal distribution (Figure 41). There are no distortions in the curve that is again characterised by a very large proportion of rare species. This tail end distribution anomaly is likely responsible for the less then perfect fit, in what otherwise resembles the perfect lognormal pattern.

7.3.2 Life Strategies

The F' of common species was quite varied (Table 17). The average F' for the common species was 27% and most species have dust seeds/spores. The duration and season of observed flowering periods for the common species was varied (Figure 42). In January, clumps had a c. 23.5% probability of having a fertile individual while in May was less than 5% (Figure 42).

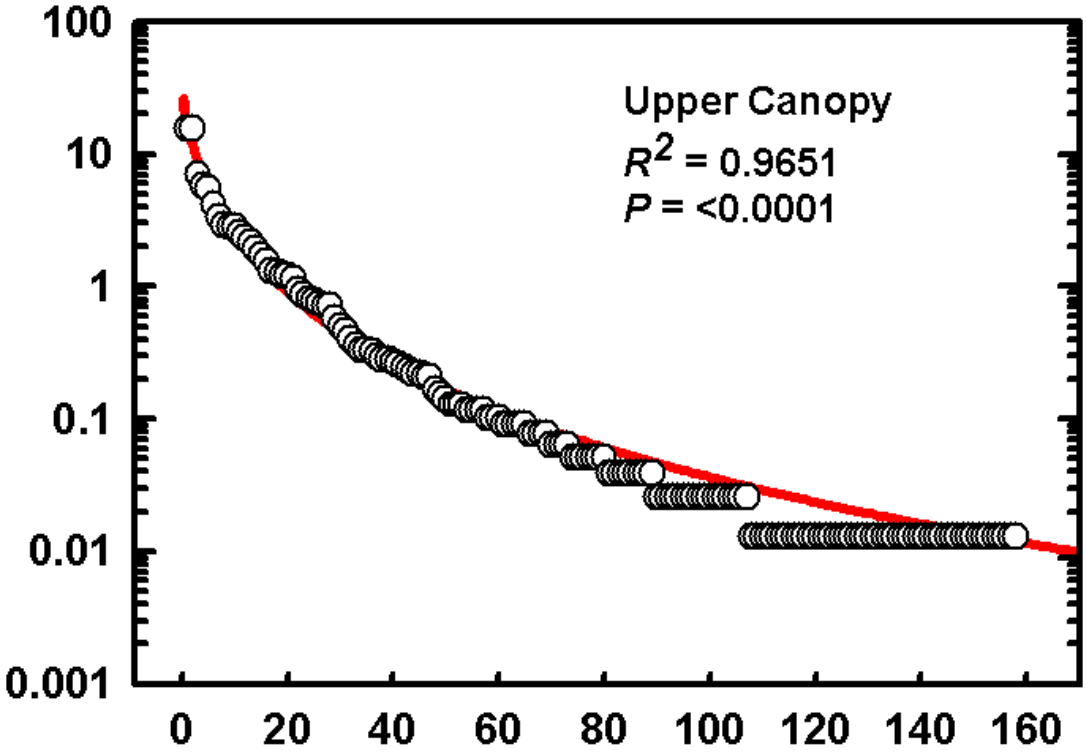


Figure 41: The dominance/diversity curve fitted to the general lognormal model for the upper canopy community. Percentage abundance on a log scale (Y) of all epiphyte species in rank order of abundance (X).

Table 17: The seed/spore type and population fertility rates (F') of the 28 common epiphyte species

	Seed/Spore	F'
Barbosella cucullata	Dust	31
Bromeliaceae sp. 01	Plume	0.06
Bromeliaceae sp. 02	Plume	0.02
Bromeliaceae sp. 03	Plume	0.5
Bromeliaceae sp. 04	Plume	0.2
Disterigma sp. *01*	Berry	27
Elaphoglossum latifolium	Dust	5
Elaphoglossum sp. *01*	Dust	54
Elaphoglossum sp. *02*	Dust	4
Elaphoglossum sp. *07*	Dust	66
Elaphoglossum sp. *09*	Dust	33
Elleanthus sp. *01*	Dust	1
Epidendrum sp. *03*	Dust	14
Lellingeria sp. *01*	Dust	48
Masdevallia sp. *01*	Dust	8
Maxillaria notylioglossa	Dust	53
Maxillaria sp. *01*	Dust	46
Maxillaria sp. *13*	Dust	50
Melpomene sp. *01*	Dust	31
Peperomia sp. *01*	Wind	53
Pleurothallis aff. *angustilabia*	Dust	25
Pleurothallis matudina	Dust	39
Pleurothallis sp. *11*	Dust	25
Pleurothallis sp. *19*	Dust	36
Prosthechea fusca	Dust	9
Scaphyglottis sp. *01*	Dust	30
Sphyrospermum sp. *01*	Berry	44
Stelis campanulifera	Dust	41

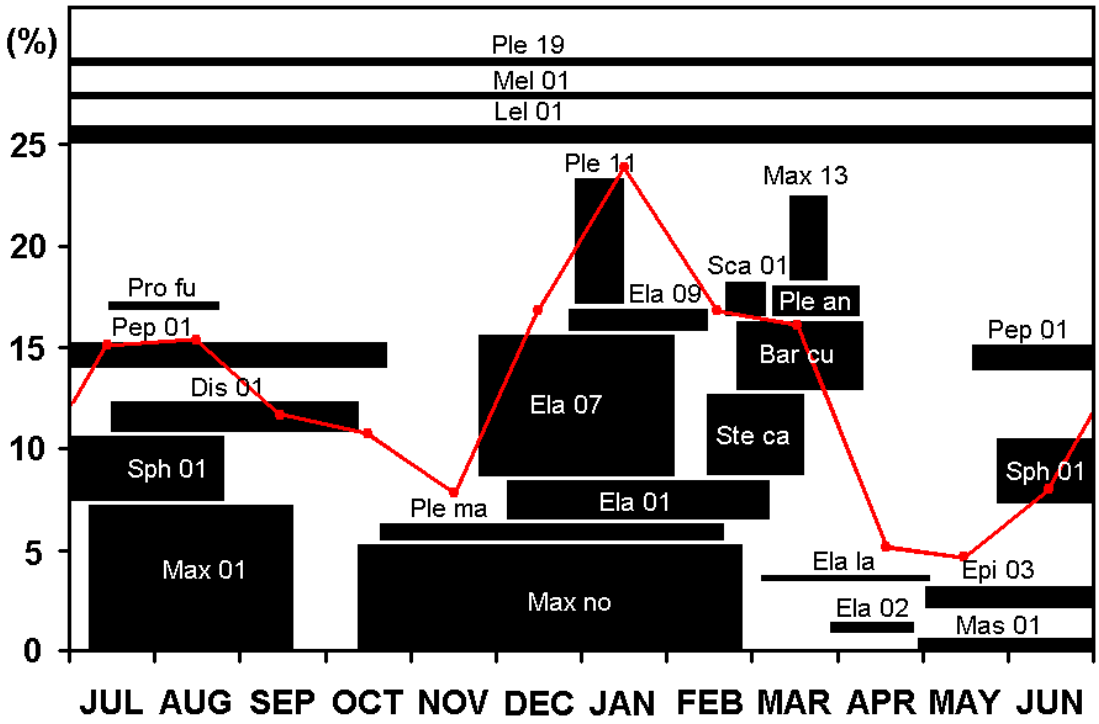


Figure 42: 1. The probability (%) of finding flowering/fertile individuals of each common species within an epiphyte clump at any time during the calendar year (only black area and Y axis for scale only). The height of the black areas are P' $_{period}$ and the area is relative to P $_{clump}$. Species codes not set within areas relate to those areas directly below. 2. The probability (%) of finding flowering/fertile individuals of any of the common species within an epiphyte clump for each month (red line).

Six pleurothallid species (except *Masdevallia* sp. 1) showed an consistently moderate F', while the three species of *Maxillaria* showed a high F'. The five sun ferns showed a high F', while the two shade ferns showed a low F'. All bromeliads showed a low F' and most miscellaneous orchids had low F'.

7.3.3 Classification

The dendrogram was trimmed at six levels to retain 15% information whilst defining some level of association between species (Figure 43). There were significant differences in the distribution between the cluster groups in Abundance per Clump, Richness per Clump, 'Other Species' per Clump, branch diameter, LAIDev, RadMidd and Johansson Zone (Table 18, Figure 44).

Groups 1 and 3 had the largest numbers of clumps. Group 1 had significantly less RadMidd and a significantly higher percentage of insignificant species and LAIDev than all other groups. Groups 1 and 2 were comprised of predominantly Zone 4 clumps. Group 3 had more individuals per clump, had a higher proportion of Zone 5 clumps, and had a significantly lower branch diameter and percentage of 'other species' than all other groups. Groups 4 and 5 were comprised of clumps from both zones and had the highest mean RadMidd values. However, Group 4 had the highest mean clump richness and abundance, whilst Group 5 had the lowest mean clump richness and abundance. Group 6 had a high proportion of Zone 5 clumps.

All species showed significant differences in percentage frequency (PF) between cluster groups, with the exception of *Scaphyglottis* sp. 1. The shade ferns *Elaphoglossum latifolium* and *E*. sp. 2, and, *Masdevallia* sp. 1 and *Peperomia* sp. 1 have their highest PF in Group 1. In Group 2, only *Elleanthus* sp. 1. and the dominant Bromeliaceae sp. 1 showed their highest PF. There were three common species absent from Group 2. Group 3 was dominated by both early colonising species of *Maxillaria,* that also showed their highest PF. Other 'sun plants' Bromeliaceae sp. 4 and *Epidendrum* sp. 3 also had their highest PF in Group 3. Forty-two percent of common species showed their highest PF in Group 4. Group 5 was dominated by of *Stelis campanulifera* and *Pleurothallis* sp. 11. Both had their highest PF in this group. There were three common species absent from Group 5. Group 6 was dominated by Bromeliaceae sp. 2 which showed its highest PF along with *Maxillaria* sp. 13. *Elaphoglossum* sp. 9 was absent from Group 6.

Whilst ANOSIM tests showed that all cluster groups were floristically different, the level of dissimilarity between some groups was higher than others. The most dissimilar groups were Group 3 and 5, whilst the most similar were Groups 1 and 2 and Groups 1 and 6.

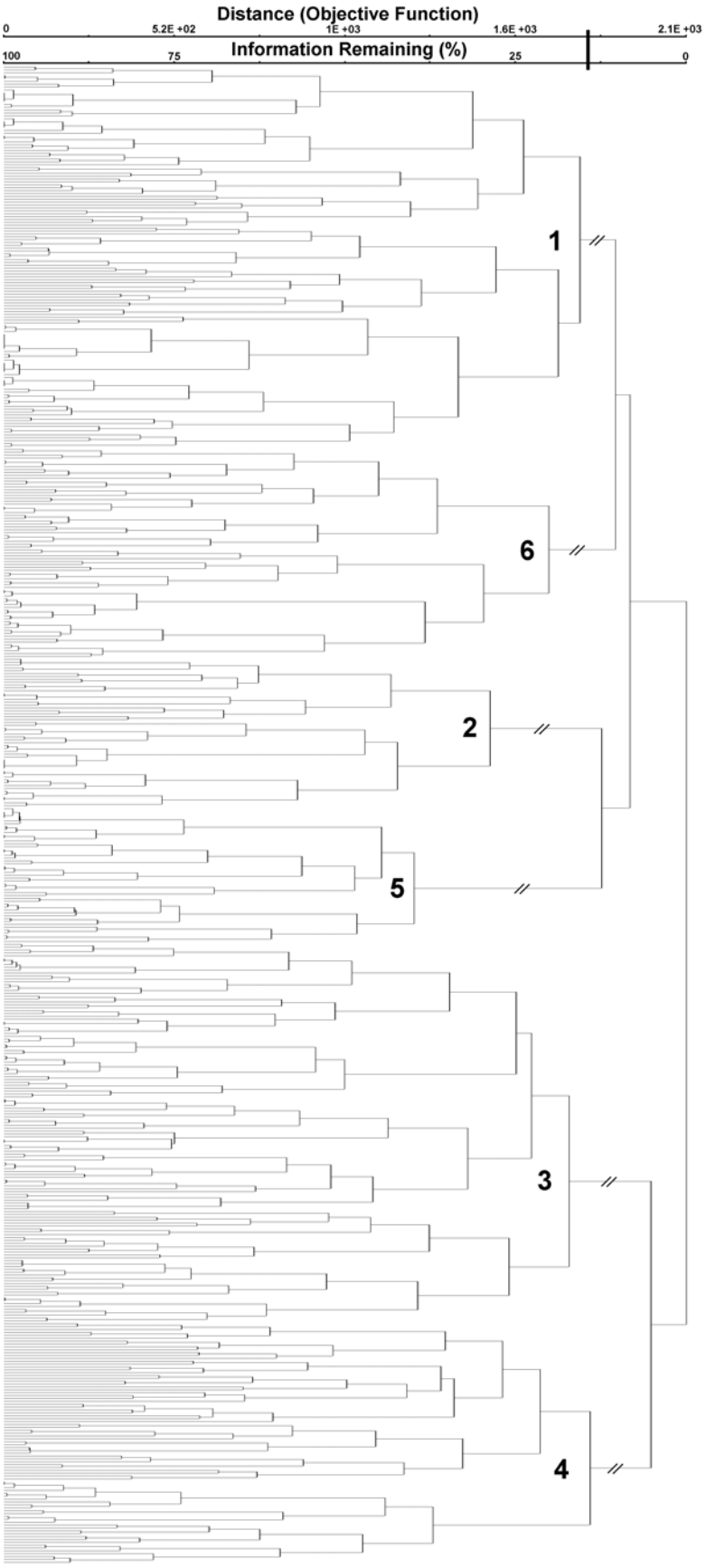


Figure 43: Dendrogram produced by the cluster analysis showing cluster groupings. The thick vertical line across the two scale bars shows the position of the trim.

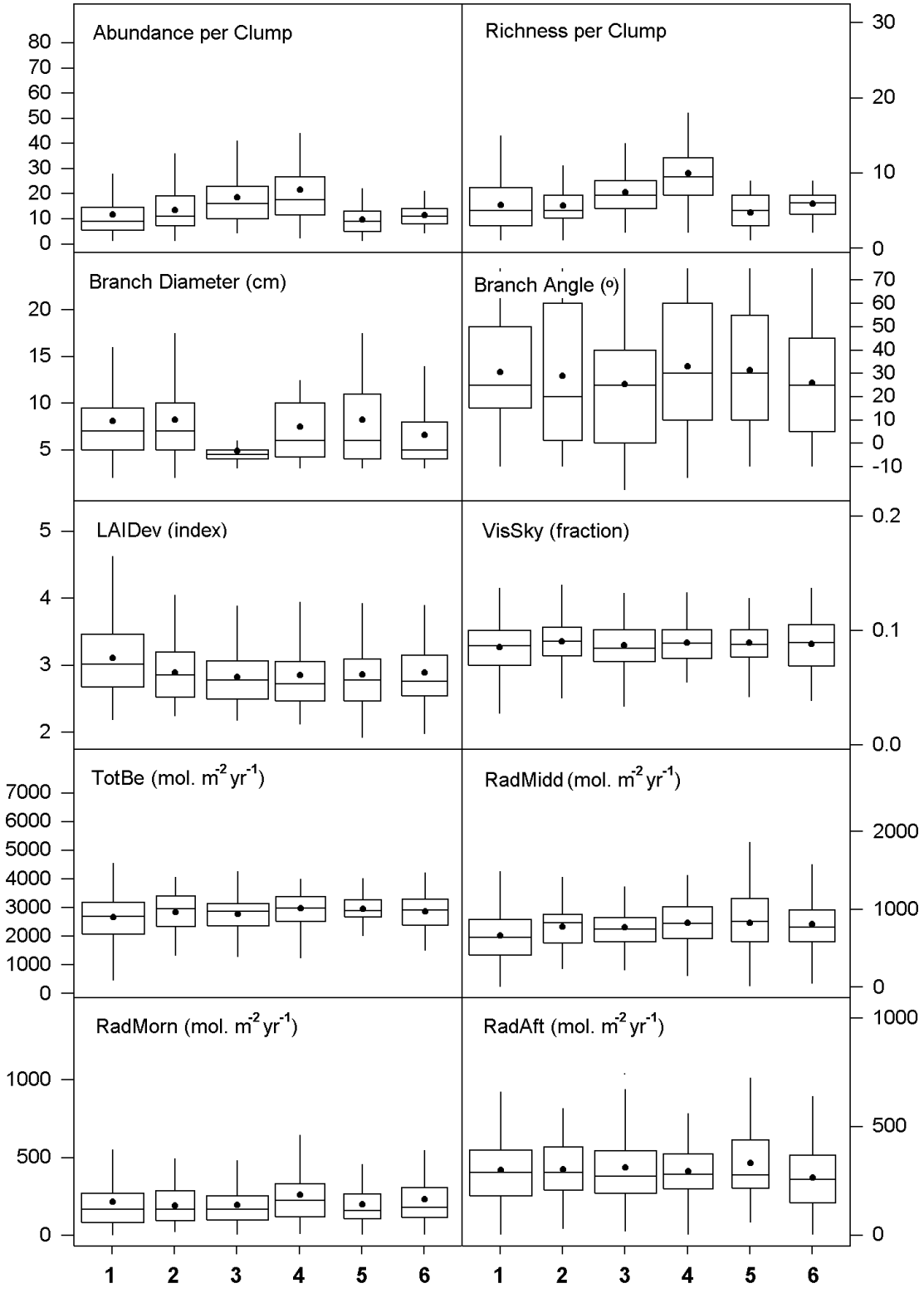


Figure 44: Boxplots of clump and environmental variables within cluster groups. Boxes represent the 2nd and 3rd quartile separated by the line at the median. Whiskers extend to the lower limits of the 1st quartile and the upper limits of the 4th quartile. Closed circles represent the mean and box width is relative to sample size.

Table 18: The means of environmental habitat variables, percentage frequency common species and results of 1-way ANOVA and contingency tables significance tests within cluster groups.

Cluster Group	1	2	3	4	5	6	
Number of clumps	**133**	**52**	**132**	**84**	**47**	**73**	
Abundance/Clump (#)	12	13.4	18.5	21.5	9.8	11.5	***
Richness/Clump (#)	5.8	5.7	7.5	10.0	4.7	5.9	***
Other species' per clump (%)	14.9	12.8	5.8	11.3	13.1	11.5	***
Branch Diameter (cm)	8.11	8.27	4.94	7.48	8.28	6.60	***
Branch Angle	30.5	28.9	25.3	33.0	31.6	26.0	NS
LAIDev (index)	3.11	2.90	2.83	2.85	2.86	2.89	***
VisSky (fraction)	0.086	0.091	0.087	0.090	0.090	0.089	NS
TotBe (mol.m2/year)	2661	2836	2788	2972	2946	2865	NS
RadMidd (mol.m2/year)	664	774	767	826	824	812	**
RadMorn (mol.m2/year)	218	192	196	263	199	232	NS
RadAft (mol.m2/year)	301	302	311	295	332	265	NS
Ratio of Zone 4 : Zone 5	**2.0 : 1**	**2.1 : 1**	**1 : 6.7**	**1.3 : 1**	**1.2 : 1**	**1 : 1.8**	***
Barbosella cucullata	**12.0**	**32.7**	**12.9**	**72.6**	**2.1**	**20.5**	***
Bromeliaceae sp. 01	**19.5**	**96.2**	**74.2**	**51.2**	**17.0**	**15.1**	***
Bromeliaceae sp. 02	**44.4**	**67**	**58.3**	**51**	**55**	**74.0**	***
Bromeliaceae sp. 03	**10.5**	**17.3**	**45.5**	**8.3**	**0.0**	**4.1**	***
Bromeliaceae sp. 04	**5.3**	**1.9**	**13.6**	**10.7**	**2.1**	**4.1**	*
Disterigma* sp. *01	**21.1**	**1.9**	**13.6**	**35.7**	**8.5**	**2.7**	***
Elaphoglossum latifolium	**23.3**	**3.8**	**1**	**11.9**	**8.5**	**5**	***
***Elaphoglossum* sp. 01**	**11.3**	**5.8**	**6.1**	**34.5**	**4.3**	**5.5**	***
***Elaphoglossum* sp. 02**	**28.6**	**2**	**3.0**	**15**	**0**	**11.0**	***
***Elaphoglossum* sp. 07**	**16.5**	**1.9**	**43.9**	**71.4**	**12.8**	**46.6**	***
***Elaphoglossum* sp. 09**	**9.8**	**0.0**	**5.3**	**14.3**	**4.3**	**0.0**	**
***Elleanthus* sp. 01**	**24.8**	**34.6**	**2.3**	**25.0**	**12.8**	**8.2**	***
***Epidendrum* sp. 03**	**6.0**	**3.8**	**35.6**	**26.2**	**6.4**	**9.6**	***
***Lellingeria* sp. 01**	**14**	**25.0**	**31.1**	**40.5**	**8.5**	**20.5**	***
***Masdevallia* sp. 01**	**21**	**9.6**	**17.4**	**15.5**	**6.4**	**5.5**	*
Maxillaria notylioglossa	**40.6**	**19.2**	**90.9**	**60.7**	**38.3**	**49.3**	***
***Maxillaria* sp. 01**	**6.8**	**3.8**	**64.4**	**44.0**	**8.5**	**63.0**	***
***Maxillaria* sp. 13**	**5**	**0.0**	**14.4**	**10.7**	**2.1**	**20.5**	***
***Melpomene* sp. 01**	**9.0**	**15.4**	**2.3**	**19.0**	**10.6**	**12.3**	**
***Peperomia* sp. 01**	**21.8**	**11.5**	**9.8**	**7.1**	**4.3**	**9.6**	**
Pleurothallis* aff. *angustilabia	**9.0**	**5.8**	**9.8**	**26.2**	**0.0**	**9.6**	***
Pleurothallis matudina	**17**	**9.6**	**1.5**	**19.0**	**4.3**	**1.4**	***
***Pleurothallis* sp. 11**	**12.8**	**26.9**	**21**	**28.6**	**55.3**	**47**	***
***Pleurothallis* sp. 19**	**18**	**5.8**	**5.3**	**19.0**	**2.1**	**6.8**	***
Prosthechea fusca	**5.3**	**5.8**	**12**	**15.5**	**6.4**	**1**	**
***Scaphyglottis* sp. 01**	**7.5**	**0.0**	**5.3**	**4.8**	**12.8**	**6.8**	**NS**
***Sphyrospermum* sp. 01**	**24.1**	**26.9**	**28.8**	**66.7**	**4.3**	**24.7**	***
Stelis campanulifera	**10.5**	**32.7**	**26.5**	**39.3**	**89.4**	**9.6**	***

Environmental Variables: 1 - way ANOVA
Binary Variables: Chi-Squared test

NS : no significant differences
*** : P < 0.05**
**** : P < 0.001**
***** : P < 0.0001**

Table 19: ANOSIM results for cluster analysis groupings. R = 0.2856 (*P* = <0.0001)

7.3.4 Ordination

The NMS ordination resulted in a three dimensional solution with a moderately high minimum stress (stress = 24.283%) and a large amount of overlap between cluster group scores (Figure 45). Further dimensions reduced stress but were within the range obtained with randomised data by the Monte Carlo test. All environmental habitat variables except RadMorn and RadAFt showed significant vectors of maximum correlation (Table 20).

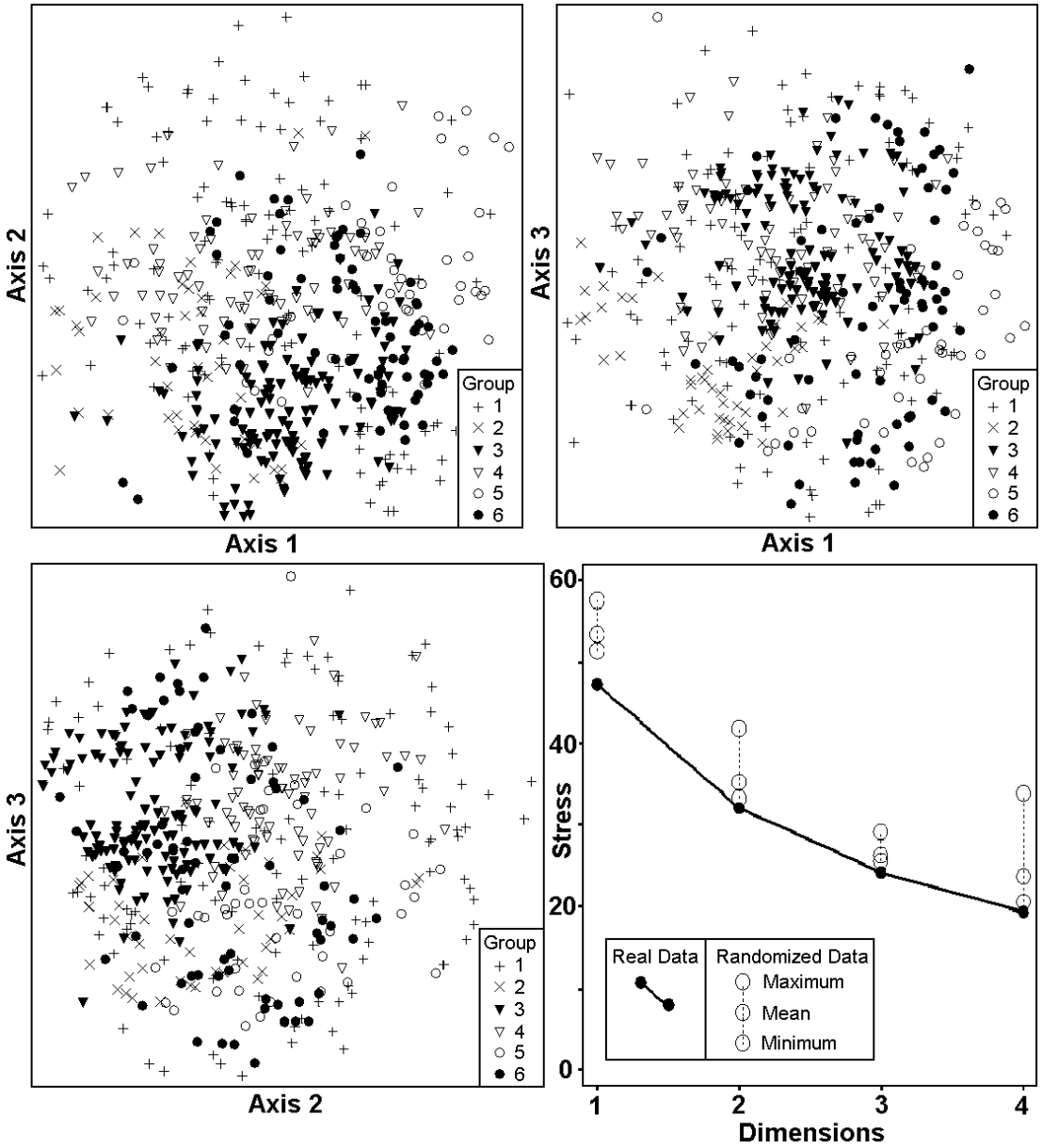


Figure 45: Non-Linear Multidimensional Scaling ordination plots of upper canopy clumps classified by cluster grouping scores and the scree plot indicating stress levels at each dimension.

Table 20: Vectors of maximum correlation for environmental habitat variables for NMS of upper canopy clumps

Variable	max R	*prob*
Zone	0.5106	*0.000*
Dia	0.4041	*0.000*
Ang	0.1891	*0.001*
LAIDev	0.2095	*0.000*
VisSky	0.173	*0.002*
TotBe	0.1652	*0.000*
RadMidd	0.1583	*0.002*
RadMorn	0.0481	*0.752*
RadAft	0.0896	*0.254*

7.3.5 Niche Overlap

The observed community mean O' was 0.19 and the mean of the simulated mean O' was 0.11 (σ^2 = 0.00001). Not a single simulated mean was greater than or equal to the community mean. The mean O' of most species was higher than the community mean O' (Figure 46).

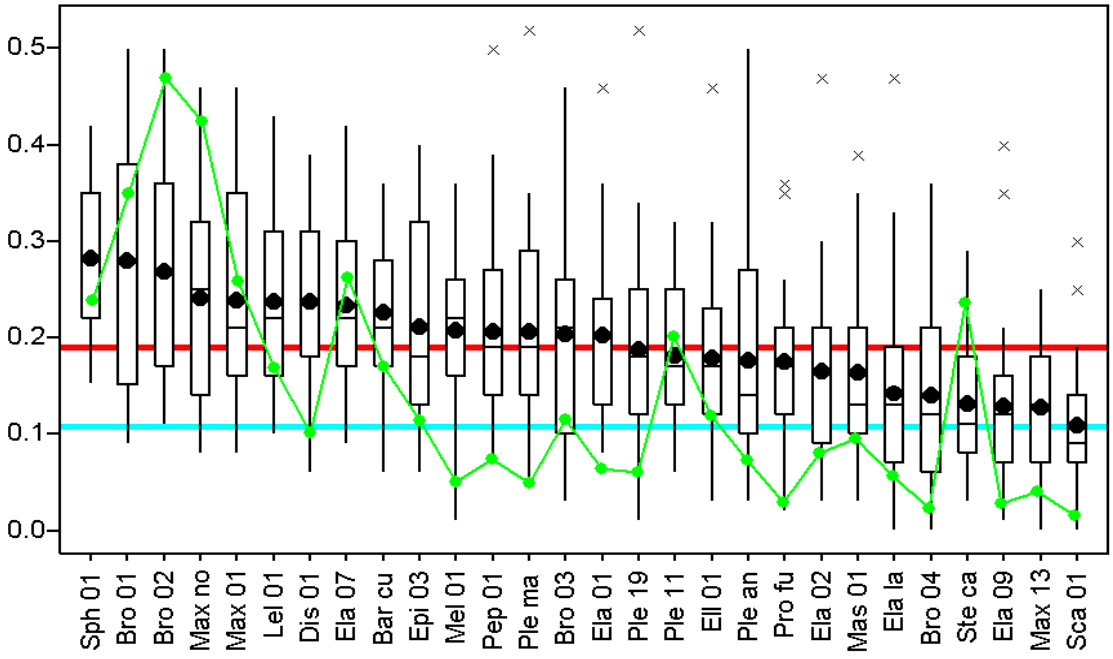


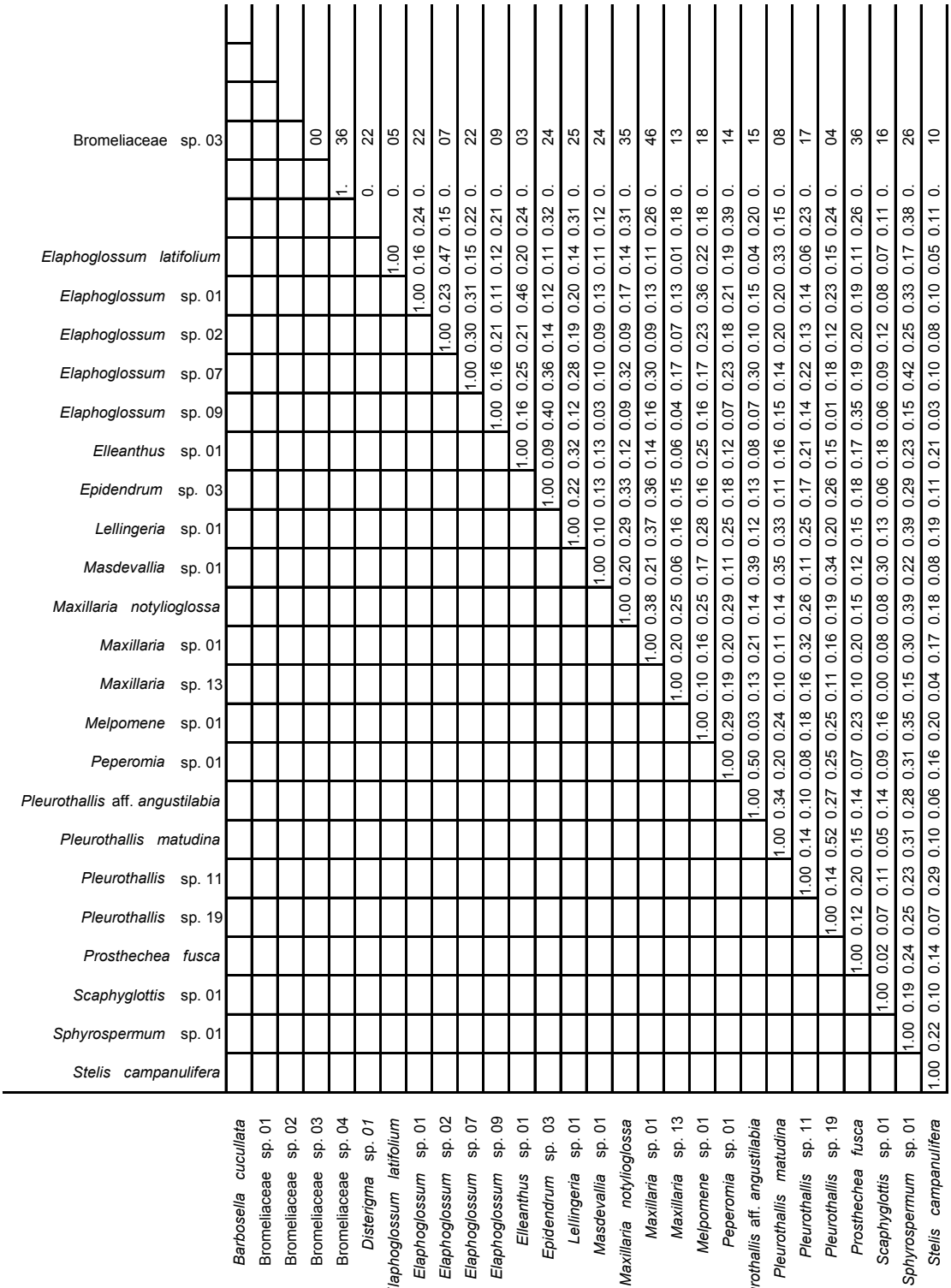
Figure 46: Boxplots of the pairwise niche overlap scores and the relative percentage frequency within clumps (green line) for each common species, the community mean niche overlap (red line) and the simulated mean niche overlap (blue line). Boxes represent the 2nd and 3rd quartile separated by the line at the median. Whiskers extend to the lower limits of the 1st quartile and the upper limits of the 4th quartile. Closed circles represent the mean and crosses are outliers. Abbreviations for common species are described in Table 21.

The Pearson correlation score between clump percentage frequency and mean niche overlap was 0.683 (P = <0.0001). All common species showed intermediate pairwise O' with at least one species (Table 21), although most showed intermediate overlap with a large suit of species (Table 22). *Pleurothallis matudina* and *P*. sp. 11 showed the highest pairwise O', *Sphyrospermum* sp. 1 had the highest mean O' and *Scaphyglottis* sp. 01 showed the lowest average O'.

Table 21: The highest pairwise niche overlap (O' - high) and corresponding species, mean niche overlap (O' – mean), and percentage frequency within clumps (PF) of common species within the upper canopy. Abbreviations relate to Figure 46.

	abbrev.	*O'* - high	and pairwise species	*O'* - mean	PF
Barbosella cucullata	Bar cu	0.36	Bromeliaceae sp. 02	**0.23**	**21.68**
Bromeliaceae sp. 01	Bro 01	0.46	*Maxillaria notylioglossa*	**0.28**	**40.35**
Bromeliaceae sp. 02	Bro 02	0.43	*Lellingeria* sp. 01	**0.27**	**52.69**
Bromeliaceae sp. 03	Bro 03	0.46	*Maxillaria* sp. 01	**0.20**	**15.98**
Bromeliaceae sp. 04	Bro 04	0.36	Bromeliaceae sp. 03	**0.14**	**6.33**
Disterigma* sp. *01	Dis 01	0.39	*Peperomia* sp. 01	**0.24**	**14.56**
Elaphoglossum latifolium	Ela la	0.47	*Elaphoglossum* sp. 02	**0.14**	**9.81**
***Elaphoglossum* sp. 01**	Ela 01	0.46	*Elleanthus* sp. 01	**0.20**	**10.60**
***Elaphoglossum* sp. 02**	Ela 02	0.47	*Elaphoglossum latifolium*	**0.17**	**12.34**
***Elaphoglossum* sp. 07**	Ela 07	0.42	*Sphyrospermum* sp. 01	**0.23**	**31.17**
***Elaphoglossum* sp. 09**	Ela 09	0.40	*Epidendrum* sp. 03	**0.13**	**6.80**
***Elleanthus* sp. 01**	Ell 01	0.46	*Elaphoglossum* sp. 01	**0.18**	**16.30**
***Epidendrum* sp. 03**	Epi 03	0.40	*Elaphoglossum* sp. 09	**0.21**	**15.82**
***Lellingeria* sp. 01**	Lel 01	0.43	Bromeliaceae sp. 02	**0.24**	**21.52**
***Masdevallia* sp. 01**	Mas 01	0.39	*Pleurothallis* aff. *angustilabia*	**0.16**	**13.92**
Maxillaria notylioglossa	Max no	0.46	Bromeliaceae sp. 01	**0.24**	**48.10**
***Maxillaria* sp. 01**	Max 01	0.46	Bromeliaceae sp. 03	**0.24**	**30.85**
***Maxillaria* sp. 13**	Max 13	0.25	*Maxillaria notylioglossa*	**0.13**	**8.23**
***Melpomene* sp. 01**	Mel 01	0.36	*Elaphoglossum* sp. 01	**0.21**	**9.18**
***Peperomia* sp. 01**	Pep 01	0.50	*Pleurothallis* aff. *angustilabia*	**0.21**	**11.71**
Pleurothallis* aff. *angustilabia	Ple an	0.50	*Peperomia* sp. 01	**0.18**	**11.55**
Pleurothallis matudina	Ple ma	0.52	*Pleurothallis* sp. 19	**0.21**	**9.02**
***Pleurothallis* sp. 11**	Ple 11	0.32	*Maxillaria* sp. 01	**0.18**	**24.84**
***Pleurothallis* sp. 19**	Ple 19	0.52	*Pleurothallis matudina*	**0.19**	**10.28**
Prosthechea fusca	Pro fu	0.36	Bromeliaceae sp. 03	**0.18**	**6.96**
***Scaphyglottis* sp. 01**	Sca 01	0.30	*Masdevallia* sp. 01	**0.11**	**5.54**
***Sphyrospermum* sp. 01**	Sph 01	0.42	*Elaphoglossum* sp. 07	**0.28**	**28.80**
Stelis campanulifera	Ste ca	0.29	*Pleurothallis* sp. 11	**0.13**	**28.48**

Table 22: Pairwise niche overlap scores using Pianka's (1973) Index for common species of the upper canopy.



7.4 Discussion

7.4.1 Community Structure

Until now, the lognormal species distributions have only been briefly discussed. The general lognormal model of species distribution was first proposed by Preston (1948). The distribution represents a community where there are many species of intermediate abundance/importance, and is particularly descriptive of species distributions of species rich communities where the factors affecting the distribution are complex (Whittaker, 1965). Hubbell (1979) argued that in tropical regions, the lognormal relative abundance pattern can represent disturbance regimes in non-equilibrium plant communities. The explanation he presented describes stochastically distributed mortality within a saturated community that results in lognormal distributions that replicate the mortality patterns seen in the epiphyte community through slumping. Thus, the lognormal distribution found in the present study may be a direct result of a stochastic species replacement mechanism.

Similar to all other previous analyses in the present study, the upper canopy dominance/diversity curve displays a large proportion of rare species in the community that creates a long tail compared to the typical lognormal distribution. As briefly discussed in previous chapters, this is not the predicted trend of logarithmic models. However, a number of more recent studies have noticed this phenomenon in similarly large assemblages (Magurran and Henderson, 2003; Nee *et al.*, 1991). Magurran and Henderson (2003) were able to show how in a fish population, the lognormal model applies to the persistent part of the community, and that when separated out, the large numbers of rare species follow a log series distribution. The latter represented the transient species of the estuarine community. There is a strong analogy to the epiphyte community in this type of distribution pattern. There is now a wealth of studies at various scales that describe how the epiphyte environment often results in populations with patchy or patchily clumped distributions (Bennett, 1986; Freiberg, 1999; Nieder *et al.*, 2000; ter Steege and Cornelissen, 1989; Tremblay, 1997; Tremblay *et al.*, 1998). This can

be defined as an environment where the probability of mortality fluctuates in correspondence to the position in the environment (Wiens, 1976). Such patchily distributed epiphyte species are analogous to the randomly occurring transient fish species found by Magurran and Henderson (2003). Similarly to the fish, there is likely to be a turnover in rare species surveyed within a given area over time. Thus, in the present study, it is suggested that the observed anomalies to the lognormal distribution might result from and be maintained by a transient (patchy) element in the species composition.

This appears be the first reporting of a long tailed lognormal trend from an epiphyte community. The only other epiphyte study known to the author that has provided dominance/diversity curves was that of Hietz and Hietz-Seifert (1995b). In that study of a more species poor community than that of the *Ficus* host, the species distribution followed a perfect lognormal trend and the tail declined sharply. In the present study, the relatively high frequency of patchily distributed species has significance for patterns of beta-diversity. Beta-diversity in lowland forests is commonly lower than that in montane areas (Nieder *et al.*, 1999). These results suggest that beta-diversity may be relatively low for a montane site, although sampling from a larger area is needed in order to assert such a claim.

7.4.2 Life Strategies

The method of dispersal contributes to the variation in both the distance that an epiphyte diaspore can travel and the type of distribution pattern seen in the population (Kessler, 2002; Madison, 1979). Whilst the method of dispersal and fertility of only the common species is discussed, some aspects typical of the rarer species also emerged from the group and are likewise discussed.

The F' for the abundant bromeliad species was extremely low. This was not surprising as the use of vegetative propagation by epiphytic bromeliads has been well documented (Benzing and Davidson, 1979; Laube and Zotz, 2003). Many of the individuals were clearly not of a reproductive age and the low F' suggests that the bromeliads rely on other mechanisms than high F', such as longevity and high fecundity for canopy dominance.

Plumed seeds of the common species were often found attached to old inflorescences in the canopy. Such seeds are an efficient method of carriage and anchorage within the epiphyte environment (Benzing, 1990) and are almost the exclusive dispersal mechanisms for bromeliads in the upper canopy (Pittendrigh, 1948). Benzing (1990) suggested that some of the more intricate coli plume seeds were so effective at entrapment that they may even create locally clumped distributions through high local entrapment.

The duration of flowering periods could not be observed for bromeliads, but in two rarer species, the development of the inflorescence from within the rossette was observed over a few months. This can be explained by the relatively large energy expenditure needed by large epiphytes for reproductive events. Benzing and Davidson (1979) showed how a bromeliad epiphyte had a flexible fruiting phenology. In the *Tillandsia* species studied, it was shown that the system of nutrient allocation was designed to minimise the time between reproductive cycles. The epiphyte would become reproductive as soon as enough resources had been collected, regardless of seasonal effects. When nutrients are limiting, epiphytes can use such strategies to use every available resource to maximise reproduction in a limiting environment.

The three dicotyledonous angiosperms displayed relatively high F', and were all dry season flowering. The two ericaceous species had berry fruits; *Disterigma* sp. 1 with flowers likely to be bee-pollinated (Snow and Snow, 1980), and *Sphyrospermum* sp. 1 with hummingbird pollinators. The dry season flowering may be explained by the increase in observed bird activity during that period. The berry fruits are dispersed by canopy birds and the dry season fruiting may also be favourable given the plethora of available terrestrial berry fruits during the wet-season. The seeds of some ericaceous epiphytes have been observed to germinate whilst still within the berry (Luteyn, 1989) This would appear to be an extreme epiphytic adaptation to maintain canopy height amongst the pitfalls between branches.

The ferns varied in phenology and F' according to family. The *Elaphoglossum* species were all fertile during the wet season, whilst the smaller graminoid species *Lellingeria* sp. 1 and *Melpomene* sp. 1 were

successively fertile year round. All of the non-shade ferns with typical canopy distributions had very high F'. In contrast, the two shade ferns showed very low F'. This may be related to the more specialised environment, where competition for space could be lower, or more likely, a result of a low photosynthetic efficiency and energy budget as found for shade ferns in a Mexican canopy (Hietz and Briones, 2001).

With the exception of *Masdevallia* sp. 1, the pleurothallid species showed a moderate F' that was consistent throughout all species. However, as this analysis covers common species only, the highly varied pleurothallids are not all likely to follow similar trends. In fact, given the large amount of rare canopy species, the high observed F' is likely to be a factor in the explanation of their high relative abundance. With the exception of one species, all were wet season flowering, which was the general trend for the majority of pleurothallids species encountered. Furthermore, the individuals of the common species had relatively longer flower duration relative to that observed for rarer species (pers. obs.). The tiny flowers are mostly pollinated by flies (van Dulmen, 2001) and the typical orchid dust seeds appear to be the most effective mechanism for avoiding clumped distributions (Madison, 1979). Many of the species of diminutive stature appeared to display a relatively higher rate of shoot growth than the large species (pers. obs.). Despite being one of the most species rich groups of orchids in the neotropics (Luer, 1986b; Vásquez and Ibisch, 2000), little is known about the reproductive ecology of the Pleurothallidinae.

All three *Maxillaria* species had relatively high F'. This is not surprising given the dynamic nature of the canopy edge. Interestingly, the two dominant species did not have overlapping flowering periods and the gap between them was months. The other orchids were quite varied. However, *Prosthechea fusca* and *Elleanthus* sp. 1, and to a lesser extent *Epidendrum* sp. 3 showed particularly low F'. These were also the largest orchids of the common species. Their large size and the poor nutrient/moisture supply of the canopy (Benzing, 1990) is likely to negatively affect growth rates (Zotz, 1995; Zotz *et al.*, 2001; Zotz and Tyree, 1996), photosynthetic efficiency (Zotz, 2000) and F' (Zimmerman and Aide, 1989). Zimmerman and Aide (1989) studied the

pattern of fruit production in the orchid *Aspasia principissa* in Panama. They found evidence that suggested that the fruiting cycle of this orchid was an expensive exercise for the individual plant. They noted that fruiting individuals were severely limited in plant growth and fruiting ability in the years to follow, implying a heavy burden on the plants resources. Ackerman and Montalvo (1990) found exactly the same result in a Puerto Rican orchid population of *Epidendrum ciliare*, and similarly, over a two year period after flowering, plant growth was significantly reduced as a result of the burden of flowering.

Many orchid species achieve energy efficiency with adaptations such as leaf shedding (Benzing, 1990; Goh and Kluge, 1991) and pseudobulbs (Figure 47). Pseudobulbs are photosynthetically active storage reservoirs for water and carbohydrates that are 'trickle fed' over long periods of time to support the orchid when supply is halted (Benzing, 1990; Goh and Kluge, 1991). In many species, pseudobulbs may take years to mature (Benzing, 1990)(e.g. *Prosthechea fusca*, pers. obs.). It is only at maturation that sufficient energy can be provided for the growth of an inflorescence in many species, upon which, over a year may pass until the dehiscence of the capsule occurs (Benzing, 1990). An extreme example of energy efficiency adaptations by canopy orchids is the photosynthetic activity by fruits (Zotz *et al.*, 2003).

Figure 47: A basal pseudobulb below the petiole in *Maxillaria* sp. 3.

The predominance of wind-dispersed diaspores in the epiphyte environment is common throughout the world, especially in the upper canopy (Kelly, 1985; Pittendrigh, 1948). The tubular flowers and berry fruits of the Ericaceae are adapted to hummingbird polination (Dziedzioch *et al.*, 2003; Snow and Snow, 1980).

7.4.2.1 Clump Fertility

Not surprisingly, the probability of flowering/fertile individuals occurring within a clump was higher during the wet season. The probability was also relatively high during the dry season despite the lower amount of flowering/fertile species. Though the timing of the peak probability in January is likely to be similar to other communities, it is not known if the clump fertility probability of c. 23.5% is high as there are no data with which to compare. Despite using only the common species, the low frequency of the rarer species could be expected to have little impact on the shown probability trends. However, irrespective of frequency, the vast majority of species flowered or were fertile during the wet season.

Within the common species, the only species displaying year round flowering/fertility are the diminutive graminoids and *Pleurothallis* sp. 19. This is likely to be a result of the far greater ability to increase the root-shoot ratio with a small plant size that could result in a higher relative uptake. Successive flowering is also characteristic of the diminutive lepanthid orchids (Luer, 1996).

Whilst fruiting cycles could not be determined in the present study, generally speaking, it is assumed that fruiting cycles would lag at a similar trend to the flowering probabilities. However, the probabilities for fruit production are likely to be lower than those for flowering due to the low pollination rates observed in some canopy epiphytes (Ackerman and Montalvo, 1990; Zimmerman and Aide, 1989).

7.4.3 Classification and Ordination

The cluster analysis identified loose epiphyte species associations that could be related to environmental variables. These included a shade group (Group 1), a small branch group (Group 3), and a third group that bears floristic resemblance to the Zone 4 low richness group identified in the previous chapter.

The shade group was environmentally defined by the significantly lower RadMidd and the far greater proportion of clumps at the lowest values of TotBe. It was floristically defined by the markedly higher PF of the only two shade ferns within the common species (*Elaphoglossum latifolium*, *E*. sp. 2) and the herbaceous *Peperomia* sp. 1. Canopy ferns often show distinct canopy distributions on the basis light (Hietz and Briones, 2001). However, of all the pairwise similarity scores between groups, not only did the shade group share the two highest similarities with Group 2 and 6, all of its similarity scores were higher than any pairwise score between any other groups. Furthermore, for most of the environmental habitat variables, the shade group range is one of, if not, the highest of all the groups. Along with the large number of clumps, these results indicate that the group is very heterogenous.

The small branch group (Group 3) was the most distinct of all the groups. It was defined by the lowest branch diameter, the highest proportion of Zone 5 clumps and by far the lowest proportion of rare species. The floristics of the group suggested that it encompassed the colonising clumps as it housed the highest PF of the two colonising species of *Maxillaria*. However, the RadMidd is the second lowest that blurs its classification as colonising. This may indicate the location of many of the clumps on the lateral and lower sides of the crown given the low branch diameter. This group has the highest floristic dissimilarities of all the groups and is the most floristically dissimilar to the shade group. Colonising clumps may be a part of the small branch group, though large number of clumps may create too much variation to allow an accurate appraisal. The group does have a relatively high abundance and richness per clump that also suggest other elements other than colonising clumps.

A third small group (Group 5), which had the most even distribution between the Johansson Zones, appeared to be floristically similar to the Zone 4 low richness group described in the previous chapter. The only species with significantly higher PF in this group than others are *Pleurothallis* sp. 11 and *Stelis campanulifera.* These two species are morphologically indeterminable without flowers, the latter being a prolific canopy generalist found in all zones. Also of significance is the lack of the humus dependent *Sphyrospermum* sp. 1. The PFs of the group are similar to the PAs observed in the low richness group of Zone 4 that was believed to be a mix of old fragmented and recolonising clumps. Likewise, Group 5 has the lowest clump richness average of all the groups and the upper quartiles of its branch diameter distribution are larger than the other groups. However, the group does have a considerably higher RadMidd relative to the Zone 4 low richness (Table 14 - Chapter 6) indicating that the clumps in both groups are likely to be different. Furthermore, the floristic dissimilarity with the small branch group is the highest of all groups.

Group 2 was defined by high branch diameter and low richness and the low PF of all *Maxillaria* and *Elaphoglossum* species. Its ecological relationships are unclear, suggesting a later successional stage. The contrasting group was Group 4, which appears to be composed of everything. This group showed the highest RadMidd, and, abundance and richness per clump. Not a single species in the group showed a low PF relative to their group distributions. This group obviously represents the majority of the very high richness clumps. This large group suggests a large number of clumps have overlapping floristics and also agrees with the assertion from the finding in the previous chapter that the high richness clumps tend to occur in areas of relatively higher PAR.

The NMS ordination and vector fitting reflected the relationships with habitat variables found in the cluster groupings. The significant differences in Johansson Zone and branch diameter of the small branch group were shown in the vector fitting. The NMS ordination plot classified by cluster grouping was included to show the definition in floristics between the cluster groupings. The NMS is generally in accordance with the cluster grouping and reinforces

that lack of convincingly different habitat characteristics of many of the groups apart from the small branch group. In light of the general hardiness and the required adaptations possessed by upper canopy epiphytes, the low influence of habitat characteristics on the species associations within the upper canopy should not be surprising.

7.4.4 Niche Overlap

The niche overlap analysis showed that the observed community mean O' was higher than a single randomised model could predict (1000 permutations). As the difference between the observed O' and the mean simulated O' was considerable, the probability of a high degree of niche overlap amongst many species is very high. However, judging by the highest pairwise O' for each species (highest pairwise O' = 0.52), it appears that no two species were inextricably linked, but that most species shared an intermediate pairwise O' (O' = 0.2 – 0.4) with a very large proportion of species. This suggests that while some structure exists in the species associations, the species composition of a large proportion of clumps is determined stochastically.

However, the results also suggest a small amount of niche diversity. The suggestions of a shade group from the cluster analysis were generally reflected by the low pairwise O' for the shade species *Elaphoglossum latifolium* and *E*. sp. 2 with the bromeliads and *Maxillaria* species. Despite the low PF of these ferns, they share one of the highest pairwise O'. In contrast, the other two species to show their highest PF within the shade cluster group, *Masdevallia* sp. 1 and *Peperomia* sp. 1, show a very low O' relative to their O' with all other species. Therefore, whilst shadowed by a large overlap of non-related species, small associations are likely to lie within the cluster groups. One example of pairwise associations not found within cluster groupings is seen by tracing the PF within the cluster groups of *Pleurothallis matudina* and *P*. sp. 19 who share the highest O' of the entire community. Their strong association was spread evenly amongst the cluster groups.

The mean O' of common species tended to be higher for species with higher PF and the two were significantly correlated. Whilst the difference in

frequency of two species has little effect on the pairwise O', if species are distributed randomly amongst clumps, well distributed species are likely to share niche space with a larger number of species than less well distributed species. Thus, if no niche diversification exists in the environment, we would expect that mean O' and PF be highly correlated. Based on this assumption, anomalies in the relationship between mean O' and PF represent something other than random species distributions for the given species.

The rank order distribution in pairwise O' and PF reflects the general randomness of clump distributions in the upper canopy. However, there are a number of PF anomalies in the rank order of distribution of O' (Figure 46). Bromeliaceae sp. 2 and *Maxillaria notylioglossa* have a considerably higher PF than all other species and under the random distribution assumption, their mean O' should be the highest. Their high frequency in the low richness and more specialised colonisation niche of the outer canopy (Table 14 - Chapter 6) increases the proportion of their non-overlapping niche area. This results in a lower than expected mean O' within the community.

In contrast, *Sphyrospermum* sp. 1 has a higher rank O' than other more frequent species. This creeping woody species that occurs in all canopy zones, appears dependent on deep humus accumulations and the moisture they provide (Benzing, 1987), typical of moisture loving ericaceous shrubs (Luteyn, 1989). It occupies little leaf space above clumps, yet its long roots often contribute disproportionately to clump stability and humus retention (pers. obs.). The niche of accumulated humus deposits occurs through out the canopy and overlaps with all niches defined by other environmental factors except branch angle. The lowest pairwise O' of *S.* sp. 1 is with *Stelis campanulifera* that also ranges throughout the canopy, but with preference for bare branches and/or thin humus accumulations. A similar scenario as described for *Sphyrospermum* sp. 1 is also likely to explain the rank order distribution of the other common ericaceous species. Though *Disterigma* sp. 1 is an erect shrub, its long humus binding roots may also assist its stability and increase its relative coexistence. The large overlap of species frequencies observed, clearly suggests a stochastic element to the distribution of species.

7.5 Conclusion

The long-tailed species abundance distributions caused by the abundance of patchily distributed species is likely to be found in other rich epiphyte communities once surveyed appropriately. These patterns are partly explained by dispersal mechanisms and lifecycles of the epiphyte species. The patterns also appear to apply on a small scale to the most species rich and dense part of the upper canopy of the present study. Within the upper canopy there appears to be an association of a relatively small number of species adapted to survival in the shade. There also appears to be a larger numbers of species associated with small diameter branches, and a small number of species particularly adapted to survival in humus deposits that may also increase clump stability and inadvertently increase the number of species with which they share niche space. Despite the loose associations, there are no two species that display complete overlap. However, many show intermediate overlapping ranges with a large number of species. This suggests that the majority of species are randomly distributed amongst the majority of clumps. In defiance of the ecological principle of competition, this demonstrates a high level of coexistence among similar species in what must be described as one of the most species rich plant communities described to date. What is yet to be clarified is whether the combined range of mechanisms described in the present study, can explain this richness, randomness and coexistence.

Chapter 8 Conclusion

The present study describes a non-equilibrium community that is very rich in similar species, relatively low in niche diversity, and subject to high rates of disturbance. The aim of this concluding chapter is to collate the evidence presented in previous chapters in order to develop a dynamic ecological model for the epiphyte community.

8.1 Ecological Models

Hutchinson (1959) first argued that competition between species led to a stable equilibrium in community structure, where the number of species is limited by the number niches. This classical equilibrium theory, known as competitive exclusion, dominated ecological thinking for several decades. Hutchinson (1961) himself was the first to challenge competitive exclusion through his observations of plankton, though it received little attention at the time. Gradually, other modifications to competitive exclusion principles were presented (Levin, 1970, 1974), and more recently, non-equilibrium models explaining species coexistence emerged (Chesson and Warner, 1981; Connell, 1978; Sale, 1977).

Benzing (1981) first addressed the coexistence of similar slow growing bromeliad epiphytes in a dry forest canopy, likening epiphyte mortality to the predation of coral fishes described by Sale (1977).

8.2 Coexistence of Similar Species

The high species richness of the *Ficus* epiphytic flora is unprecedented. It is comprised of a diverse range of vascular plants, yet half of the species are highly related and come from a small number of genera. At the colonisation zone of the outer branch tips, evidence of competition was found, in that a few species dominated and some were absent. Away from this outer zone of the tree, there are distinct environmental zones that provide a number of niches for epiphyte species. Yet, the species composition of these niches shows a large overlap and the species diversity that could be attributed

to most niches was large. The composition of many of the epiphyte clumps appeared to be determined randomly and most species showed an even amount of overlap. The clumps with the greatest numbers of individuals and species did not appear to lack the colonising species. Thus, there was no evidence that could support a competitive exclusion theory.

Clearly, epiphyte clumps are non-equilibrium communities, with a high degree of species coexistence. There are a number of non-equilibrium theories, each related to different environmental and ecological mechanisms that prevent niche dominance by a species. There is a large range of possible mechanisms that might prevent dominance in the epiphyte community of the present study.

8.2.1 Mechanisms of Coexistence

Disturbance Regimes

Epiphytes are prone to slumping from branches caused by wind and animal foraging throughout the year. The risk of epiphyte slumping appears to be increased in larger clumps. Slumping can cause the complete loss or fragmentation of epiphyte clumps. A higher amount of loss and fragmentation was assumed on the wider and more inclined branches of the inner canopy, based on the relative lack of, and small size of, the clumps found therein. This phenomenon is likely to be related to the crown architecture and smooth bark of the *Ficus* host. The slumping of clumps appeared mostly unrelated to the species composition of the clumps although the highest mean overlap by *Sphyrospemum* sp. 1 could have been influenced by its capacity for anchorage through its long branch encircling roots. Often, some humus may remain after slumping to allow recolonisation by a wider range of vascular species than are found on branch tips (Figure 48).

The mostly random slumping events affect mortality and colonisation. High mortality rates in epiphyte communities have been previously suggested to be an important mechanism for the maintenance of diversity (Bennett, 1986; Hietz, 1997). Whilst sampling from the canopy, the observation was made that practically no large epiphytes were found dead within the canopy.

Whilst mortality is generally high for very young epiphytes (Benzing, 1981; Hietz, 1997; Hietz *et al.*, 2002; Larson, 1992), it appeared that once large epiphytes were established in the *Ficus*, random slumping throughout mature populations was the principal source of mortality, as inferred by others (e.g. Zotz, 1995). Therefore, random mortality appears to present a mechanism that prevents exclusion by competitive species.

In a community without high rates of epiphyte slumping, it might be expected that the older clumps on inner branches be dominated by larger and different species to those in the younger clumps on outer branches (Rudolph *et al.*, 1998). However, in the *Ficus* host, the risk of slumping is higher in larger and heavier (older) clumps as a result of the smooth bark. Canopy grazers such as the brown woolly monkey, add a semi-random element to the slumping. These two mechanisms prevent exclusion by competitive species. The allocation of establishment opportunities varies both spatially and temporally within the tree, and older communities (potentially more competitive), regardless of their location, would appear to be at a greater risk of slumping.

Figure 48: Remnants of vascular plant roots (*Sphyrospermum* sp. 1), humus and bryophytes after slumping.

Diversity of Flowering Phenologies

Few species displayed very high fertility rates within their populations and the flowering periods for some common species were short.

Furthermore, the flowering periods only moderately overlapped. These suggested that at most times of the year, only a fraction of the total individuals/species in the canopy were in flower. The fruiting cycles of the epiphytes species are likely to lag on the same seasonal pattern, although the low pollination rates associated with the canopy environment (Ackerman and Montalvo, 1990; Zimmerman and Aide, 1989) are likely to severely reduce the fruiting fertility rates.

A common epiphyte adaptation is rapid growth in seedlings (Hietz *et al.*, 2002). Establishment opportunities in the canopy are normally colonised rapidly by the adjacent species (Ackerman *et al.*, 1996; Madison, 1979). Given that establishment opportunities can arise at any time, the variation of phenology and fertility amongst coexisting species creates another random mechanism to prevent exclusion by competitive species.

Age structured Community

The epiphyte community appears to consist of a range of different age and size species. The majority of the large and long-lived species had a relatively low fertility when compared to smaller species, the smallest of which show successive flowering. The relatively low fertility in larger epiphytes, like many other size-related physiological differences observed in epiphytes (Zotz, 1995; Zotz *et al.*, 2001; Zotz and Thomas, 1999), is likely to be a result of the canopy environment that imposes different levels of stress on small and large epiphytes (Zotz *et al.*, 2001). Whilst low fertility species might appear at a disadvantage in the dynamic canopy, the population of low fertility epiphytes is sustained (albeit in relatively low abundances) through a relatively high longevity (Cooper, 1946). This relaxes the establishment pressures faced by short-lived species. Providing that ample space is available over a life cycle, a low fertility and high longevity is likely to provide similar establishment probabilities to that observed in highly fertile and short-lived species. Thus, the age structure of the community has a partitioning effect. This changes the relative importance of establishment, stratifies the effects of short-term dynamic events such as drought, and creates more niche space than would otherwise be available.

Environmental Variability

The annual rainfall variability during the wet season is particularly high (Figure 4 - Chapter 2). There are no accounts of rainfall variability from other epiphyte environments known to the author and the variability may be typical of leeward cloud forests of central Peru. Whilst monthly rainfall fluctuations are a climatic norm, the wet-season minima described here may have a high significance for atmospheric plants. Epiphyte communities with remotely comparable densities and diversities to the present study have mostly been found in areas of very high rainfall (Bussmann, 2001; Gentry and Dodson, 1987b).

A number of species (common and uncommon) appeared to have short flowering periods. In many of the fecund pleurothallids, the inflorescence forms slowly over several months, before a mass release of flowering over days to weeks (pers. obs.). This is likely to be a result of their lack of pseudobulbs, storage facilities or leaf abortion characteristics other than velamenous roots (Benzing *et al.*, 1983; Benzing and Pridgeon, 1983). This suggests that this diverse and abundant group of species and others similar may be particularly dependant on ample water supply throughout the long formation of the inflorescence. This suggestion was observed during a particularly dry period in September, when the population of the early flowering *Stelis* sp. 2 appeared to suffer high plant mortality in the individuals where young inflorescences were being formed (pers. obs.).

Likewise, it was noted above that large epiphytes with a low fertility were likely to persist in the dynamic community through differences in stress tolerance. This implies that age structure is most effective in niche partitioning when environmental variability is high. The observed wet season rainfall variability suggests that it is likely that groups of similar species may be regularly prevented from completing reproductive cycles and/or suffer higher mortality (in smaller species). This would advantage larger and less fertile species that have larger storage facilities. Stochastic dry periods throughout the typical wet season is very likely to affect the dynamics of the community and may be a highly influential factor for the observed species richness of the

Ficus epiphytic flora.

Whilst environmental variability *per se* is a common phenomenon, the duration of anomaly is likely to be the key factor for the influence on species richness. The observations from the Peruvian location are essentially short and sharp spurts of drought conditions that have not been recorded over entire seasons. The duration and variation in the timing of drought does not enforce the exclusion of drought intolerant species, though reproductive cycles can be negatively affected. Thus, on a regular basis, reproductive cycles are negatively affected in randomly selected cohorts of similar epiphytes with sufficient variability in the timing as to prevent local extinctions.

8.2.2 Overview

The factors influencing the structure and species diversity of this species rich non-equilibrium community are complex and intertwined. Some of the proposed mechanisms bear similarity to the mechanisms proposed for coexistence in other communities. The stochastic distribution of establishment space allocation through epiphyte slumping is similar to the wave action disturbance found in intertidal algal communities (Dayton, 1971, 1975), the predation in reef fishes (Sale, 1977) and tree fall in tropical rainforests (Connell, 1978). Random disturbance events provide establishment opportunities in a lottery fashion to recruits of existing cohorts in many communities (Benzing, 1981; Busing and Brokaw, 2002; Hatfield *et al.*, 1996; Munday, 2004). In the context of the present study, lottery establishment allows an equal chance of establishment to any fecund species in the proximity and at the time of the slumping event.

The greater risk of mortality to older and heavier sections of the community preventing dominance by more competitive species is similar to the size-related slumping mechanism found in rock cliff dwelling plant communities (Coates and Kirkpatrick, 1992). Furthermore, Yu ad Wilson (2001) showed how coexistence is aided by spatial variation in patch density among species, which relates directly to the random spatial distribution of establishment opportunities in the present study.

The coexistence of species through the variation in fertility and phenology is supported by various hypothesis of species coexistence from a range of communities and empirical models (Aarssen, 1992; Chesson, 2000; Chesson and Warner, 1981; Hurtt and Pacala, 1995). The effect of environmental variation and the age structuring of the community has been show empirically to support coexistence (Dewi and Chesson, 2003; Hurtt and Pacala, 1995).

The variation in epiphyte fertility and phenology, community age structure and temporal climatic conditions, each create significant temporal heterogeneity in the size and species diversity of reproductive cohorts. These diverse cohorts are then presented with the lottery of establishment opportunity through epiphyte slumping. It is proposed that these combined mechanisms are responsible for the species coexistence and diversity of the immense order of magnitude described in the present study.

8.3 Conclusion

The present study has provided some novel results and insights. The epiphyte species richness is the highest ever recorded from a single tree, a record that would still stand if only the orchids were included. The large proportion of rare species highlights the patchy distribution of a very high proportion of epiphyte species.

The concentration of epiphyte individuals, species and clumps in the outermost part of the canopy had not been previously reported. This was linked to the architecture and smooth bark of the *Ficus* host, whilst reflecting the cloudiness of the site and the suitability of the outer canopy for epiphytes relative to lowland rainforest canopies. The distribution also resulted in the thickening of the outer canopy of the *Ficus* host with epiphyte plants and organic material that significantly ameliorated the outer canopy climate. This epiphytic thickening acts as like a wet blanket at the top of the canopy, both cooling daytime temperatures through moisture release and warming nocturnal temperatures through heat retention.

The influence of slope on the formation and maintenance of a broken forest canopy was shown to influence the distributions of forest microclimate and epiphytes. Though some theory of the influence of slope on forest canopy structure existed, there was little evidence to show how this affected microclimate. Subsequently, a hypothesis of nocturnal cooling was presented to explain the patterns found within the present study that may have consequences for the spatial distribution of plants in montane forests.

The succession of the epiphyte community appeared to be prevented by epiphyte slumping and the dense concentrations of larger and older plants in the inner canopy found in other locations was absent. The fringe of the outer canopy appears to provide a colonisation niche for some epiphytes, and some species associations were found on smaller diameters and in the more deeply shaded areas of the canopy. However, the majority of the clumps away from these environments were indistinguishable floristically, representing a large overlap of niche space and a high coexistence of similar species.

Whilst high epiphyte diversity is associated with humid climates, the present study is an example of how the most diverse epiphyte communities are not necessarily associated with the most humid sites, as is generally believed. The complex interactions of many mechanisms appears to foster a very high epiphyte diversity. Epiphyte slumping may operate similarly under perhumid conditions, though the other mechanisms described above may have their greatest influence on species richness and coexistence under a variable climate.

The present study has thoroughly described many aspects of an epiphyte environment from an essentially undescribed bioregion. Despite being the largest remaining tract of untransformed vegetation within the richest biological region in the world[3], the Andean forests of central Peru, are in critical danger from rampant and unchecked development at alarming rates.

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[3] Contrary to popular belief, the tropical Andes is home to a larger amount of plants (c. 45,000) and vertebrates (3,389) than the Amazon Basin (Henderson *et al.* 1991; Myers *et al*. 2000).

The present study highlights the potential biodiversity of a region that is mostly unstudied and unprotected. Further research initiatives are vital to establishing conservation priorities within the region.

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Appendix I

List of taxa found on the surveyed tree. Lifeform abbrev. and frequency values are defined in the text. All vouchers / specimens in cultivation are housed at OXA.	Lifeform	Cl. Freq. (%)	Rel. Freq. (%)
Araceae			
Anthurium incurvatum Engl. (D.Catchpole 1519)	Clb	0.8	0.06
A. sp 01 (D.Catchpole 0963)	Clb	0.5	0.04
Philodendrum sp 01 (D.Catchpole 0945)	Clb	0.5	0.06
Araliaceae			
Schefflera sp 01 (D.Catchpole 1377)	Clb	0.2	0.02
Aspleniaceae			
Asplenium radicans L. (D.Catchpole 0952)	SCr	0.8	0.11
A. sp 01 (D.Catchpole 0954)	LCr	0.2	0.01
Bromeliaceae			
cf. Bromeliaceae sp 01 (D.Catchpole 1523)	OTa	40.3	6.53
cf. Bromeliaceae sp 02 (D.Catchpole 0090)	OTa	52.7	14.82
cf. Bromeliaceae sp 03 (D.Catchpole 0046)	OTa	16.0	2.02
cf. Bromeliaceae sp 04 (D.Catchpole 0050)	OTa	6.3	0.63
cf. Bromeliaceae sp 05 (D.Catchpole 0167)	CTa	0.2	0.02
cf. Bromeliaceae sp 06 (D.Catchpole 0190)	CTa	0.8	0.12
cf. Bromeliaceae sp 07 (D.Catchpole 0280)	OTa	0.3	0.02
cf. Bromeliaceae sp 08 (D.Catchpole 0264)	OTa	0.2	0.01
cf. Bromeliaceae sp 09 (D.Catchpole 1217)	OTa	4.0	0.34
cf. Bromeliaceae sp 10 (D.Catchpole 0396)	OTa	1.1	0.08
cf. Bromeliaceae sp 11 (D.Catchpole 0432)	OTa	1.9	0.22
cf. Bromeliaceae sp 12 (D.Catchpole 0454)	CTa	0.3	0.02
cf. Bromeliaceae sp 13 (D.Catchpole 1265)	OTa	0.2	0.01
cf. Bromeliaceae sp 15 (D.Catchpole 1168)	OTa	1.3	0.14
cf. Bromeliaceae sp 16 (D.Catchpole 1023)	CTa	1.9	0.20
cf. Bromeliaceae sp 17 (D.Catchpole 1778)	OTa	0.2	0.01
cf. Bromeliaceae sp 18 (D.Catchpole 0553)	OTa	0.2	0.01
Crassulaceae			
cf. Crassulaceae sp 01 (D.Catchpole 1212)	R	0.2	0.01
Dryopteridaceae			
Elaphoglossum erinaceum (Fee) Moore (D.Catchpole 1192)	SCr	0.2	0.01
E. latifolium (Sw.) John Sm. (D.Catchpole 1290)	LCr	9.8	1.49
E. vittariodes Mickel (D.Catchpole 1379)	Pnd	2.1	0.32
E. muscosum (Sw.) Moore (D.Catchpole 1236)	LCr	0.6	0.08
E. sp 01 (D.Catchpole 0032)	SCr	10.6	0.86
E. sp 02 (D.Catchpole 1516)	LCr	12.3	1.21
E. sp 03 (D.Catchpole 0877)	LCr	0.5	0.04
E. sp 05 (D.Catchpole 1526)	SCr	2.5	0.21
E. sp 06 (D.Catchpole 0226)	SCr	0.2	0.07

Appendix I (cont)

List of taxa found on the surveyed tree. Lifeform abbrev. and frequency values are defined in the text. All vouchers / specimens in cultivation are housed at OXA.	Lifeform	Cl. Freq. (%)	Rel. Freq. (%)
Dryopteridaceae (cont.)			
Elaphoglossum sp 07 (D.Catchpole 1525)	SCr	31.2	3.82
E. sp 08 (D.Catchpole 0191)	SCr	0.3	0.02
E. sp 09 (D.Catchpole 1243)	LCr	6.8	0.81
Ericaceae			
Disterigma sp 01 (D.Catchpole 0101)	Asc	14.6	1.23
Psammisia sp 01 (D.Catchpole 0475)	Clb	0.5	0.03
P. sp 02 (D.Catchpole 0962)	Clb	0.8	0.06
Sphyrospermum sp 01 (D.Catchpole 0015)	LRp	28.8	2.54
S. sp 02 (D.Catchpole 0537)	LRp	3.5	0.24
cf. Ericaceae sp 01 (D.Catchpole 0214)	Asc	3.6	0.27
cf. Ericaceae sp 02 (D.Catchpole 0253)	Pnd	3.6	0.27
cf. Ericaceae sp 03 (D.Catchpole 0875)	Asc	1.3	0.10
cf. Ericaceae sp 04 (D.Catchpole 0939)	Pnd	0.5	0.03
Grammitidaceae			
Cochlidium sp 01 (D.Catchpole 0816)	SCr	0.6	0.04
Grammitis sp 01 (D.Catchpole 0836)	SCr	0.2	0.01
Lellingeria subsessilis (Baker) AR Sm. & RC Moran (D.Catchpole 0590)	LCr	1.3	0.19
L. sp 01 (D.Catchpole 0937)	SCr	21.5	2.18
L. sp 02 (D.Catchpole 1221)	SCr	0.5	0.03
L. sp 03 (D.Catchpole 0953)	SCr	0.2	0.01
Melpomene sp 01 (D.Catchpole 1056)	SCr	9.2	0.70
M. sp 02 (D.Catchpole 0335)	SCr	4.7	0.37
M. sp 03 (D.Catchpole 1259)	SCr	0.3	0.02
Terpsichore lanigera (Desv.) C.V.Morton sp 01 (D.Catchpole 1197)	SCr	0.2	0.01
Hymenophyllaceae			
Hymenophyllum sp 01 (D.Catchpole 1371)	FF	1.4	0.20
H. sp 02 (D.Catchpole 1521)	FF	0.5	0.07
Orchidaceae			
Barbosella cucullata (Lindl.) Schltr. (D.Catchpole 1487)	Cae	21.7	2.59
Cryptocentrum inaequisepalum C. Schweinf. (D.Catchpole 1418)	Cae	0.2	0.01
C. sp 01 (D.Catchpole 1447)	Cae	0.3	0.04
Dichaea sp 01 (D.Catchpole 0511)	Asc	2.1	0.22
Dryadella sp 01 (D.Catchpole 1188)	Asc	0.2	0.01
Elleanthus sp 01 (D.Catchpole 0031)	Cae	16.3	1.83
Epidendrum mancum Lindl. (D.Catchpole 1472)	Asc	1.4	0.11
E. aff. *miradoranum* (D.Catchpole 1286)	Asc	0.5	0.06
E. sp 01 (D.Catchpole 0610)	Asc	0.6	0.06
E. sp 03 (D.Catchpole 1028)	Cae	15.8	1.88

Appendix I (cont)

List of taxa found on the surveyed tree. Lifeform abbrev. and frequency values are defined in the text. All vouchers / specimens in cultivation are housed at OXA.	Lifeform	Cl. Freq. (%)	Rel. Freq. (%)
Orchidaceae (cont.)			
Epidendrum sp 04 (D.Catchpole 0611)	Asc	0.2	0.01
Fernandezia subbiflora Ruiz & Pav (D.Catchpole 1249)	Asc	0.2	0.06
L. aff. *mucronata (D.Catchpole 0989)*	Lep	0.3	0.02
L. sp 01 (D.Catchpole 0937)	Lep	0.2	0.01
L. sp 02 (D.Catchpole 0880)	Lep	0.2	0.01
L. sp 04 (D.Catchpole 1528)	Lep	0.2	0.01
L. sp 05 (D.Catchpole 1211)	Lep	0.2	0.02
L. sp 06 (D.Catchpole 0997)	Lep	0.3	0.03
L. sp 07 (D.Catchpole 1089)	Lep	0.2	0.04
L. sp 08 (D.Catchpole 1323)	Lep	0.9	0.12
L. sp 10 (D.Catchpole 1045)	Lep	0.2	0.01
L. sp 11 (D.Catchpole 1090)	Lep	0.2	0.01
Lepanthopsis aff. *acuminata* (D.Catchpole 1160)	Lep	0.2	0.01
Masdevallia sp 01 (D.Catchpole 0956)	Cae	13.9	2.74
M. sp 02 (D.Catchpole 1476)	Cae	0.2	0.04
Maxillaria notylioglossa Rchb. f. (D.Catchpole 1169)	LRp	48.1	14.78
M. sp 01 (D.Catchpole 0320)	LRp	30.9	5.34
M. sp 02 (D.Catchpole 0123)	LRp	0.2	0.03
M. sp 03 (D.Catchpole 0582)	Asc	1.3	0.12
M. sp 04 (D.Catchpole 1469)	Asc	0.3	0.02
M. sp 05 (D.Catchpole 0513)	Asc	0.2	0.01
M. sp 06 (D.Catchpole 1305)	Asc	0.2	0.02
M. sp 08 (D.Catchpole 1464)	LRp	1.6	0.13
M. sp 09 (D.Catchpole 1468)	LRp	3.5	0.34
M. sp 10 (D.Catchpole 0526)	Asc	0.3	0.03
M. sp 13 (D.Catchpole 0933)	LRp	8.2	0.88
M. sp 14 (D.Catchpole 0900)	Asc	2.1	0.24
M. sp 15 (D.Catchpole 1169)	Asc	0.2	0.01
M. sp 16 (D.Catchpole 1056)	Asc	0.2	0.01
Myoxanthus affinoides Luer (D.Catchpole 1264)	LRp	0.8	0.10
M. speciosus (Luer) Luer (D.Catchpole 0807)	Cae	3.2	0.25
Octomeria sp 01 (D.Catchpole 1125)	Pnd	3.6	0.34
Oncidium pastorellii Dodson&Bennett (D.Catchpole 1503)	Asc	0.2	0.01
O. retusum Lindl. (D.Catchpole 1457)	Asc	0.3	0.02
O. sp 01 (D.Catchpole 1181)	Asc	0.2	0.01
O. sp 02 (D.Catchpole 1218)	Asc	1.1	0.19
Pachyphyllum sp 01 (D.Catchpole 1518)	Asc	0.2	0.02
Platystele oxyglossa (Schltr.) Garay (D.Catchpole 0917)	Cae	0.8	0.10

Appendix I (cont)

List of taxa found on the surveyed tree. Lifeform abbrev. and frequency values are defined in the text. All vouchers / specimens in cultivation are housed at OXA.	Lifeform	Cl. Freq. (%)	Rel. Freq. (%)
Orchidaceae (cont.)			
Pleurothallis aff. *angustilabia* (D.Catchpole 0882)	Cae	11.6	1.87
P. aff. *angustilabia* 2 (D.Catchpole 1384)	Cae	0.2	0.04
P. cordata (Ruiz&Pavon) Lindl. (D.Catchpole 0386)	Cae	0.2	0.01
P. aff. *cordata* (D.Catchpole 0899)	Cae	0.2	0.01
P. grandiflora Lindl. (D.Catchpole 1506)	Cae	0.2	0.03
P. matudina C. Schweinf. (D.Catchpole 1477)	Cae	9.0	1.15
P. vestigipetala Luer (D.Catchpole 1383)	SRp	0.2	0.01
P. sp 01 (D.Catchpole 1226)	Cae	0.2	0.01
P. sp 02 (D.Catchpole 0566)	Cae	0.2	0.03
P. sp 03 (D.Catchpole 0621)	Cae	0.5	0.03
P. sp 04 (D.Catchpole 0946)	Cae	2.1	0.28
P. sp 05 (D.Catchpole 1417)	Cae	0.5	0.04
P. sp 06 (D.Catchpole 1180)	Cae	0.3	0.03
P. sp 07 (D.Catchpole 1301)	Cae	0.2	0.02
P. sp 08 (D.Catchpole 1372)	Cae	0.2	0.04
P. sp 09 (D.Catchpole 1304)	Cae	0.9	0.11
P. sp 11 (D.Catchpole 0184)	SRp	24.8	3.23
P. sp 12 (D.Catchpole 0547)	Cae	0.2	0.01
P. sp 14 (D.Catchpole 0021)	Cae	1.6	0.16
P. sp 16 (D.Catchpole 0577)	Cae	0.2	0.01
P. sp 17 (D.Catchpole 1363)	Cae	0.2	0.01
P. sp 18 (D.Catchpole 0602)	Cae	0.2	0.01
P. sp 19 (D.Catchpole 0755)	Cae	10.3	2.72
P. sp 21 (D.Catchpole 1033)	Cae	0.6	0.08
P. sp 22 (D.Catchpole 1039)	Cae	0.3	0.02
P. sp 23 (D.Catchpole 1040)	Cae	0.2	0.01
P. sp 24 (D.Catchpole 0958)	Cae	0.2	0.01
P. sp 25 (D.Catchpole 0232)	Cae	0.2	0.01
P. sp 26 (D.Catchpole 0761)	Cae	0.3	0.04
P. sp 27 (D.Catchpole 0762)	Cae	0.2	0.01
P. sp 28 (D.Catchpole 0763)	Cae	0.2	0.01
P. sp 30 (D.Catchpole 0576)	Cae	0.2	0.01
P. sp 35 (D.Catchpole 1383)	Cae	1.1	0.11
Prosthechea fusca (Schltr.) D.E. Benn. & Christenson (D.Catchpole 0029)	Cae	7.0	0.63
Scaphyglottis sp 01 (D.Catchpole 278)	Asc	5.5	0.48
Stelis aviceps Lindl. (D.Catchpole 0440)	Cae	0.2	0.01
S. campanulifera Lindl. (D.Catchpole 1451)	SRp	28.5	5.62
S. concaviflora C. Schweinf. (D.Catchpole 0492)	Cae	0.2	0.01

Appendix I (cont)

List of taxa found on the surveyed tree. Lifeform abbrev. and frequency values are defined in the text. All vouchers / specimens in cultivation are housed at OXA.	Lifeform	Cl. Freq. (%)	Rel. Freq. (%)
Orchidaceae (cont.)			
Stelis aff. *concaviflora* (D.Catchpole 1062)	Cae	0.2	0.01
S. flexuosa Lindl. (D.Catchpole 1105)	Cae	4.3	0.60
S. pusilla H.B.K. (D.Catchpole 0198)	SRp	2.2	0.18
S. rutrum Luer & Vasquez (D.Catchpole 1461)	LRp	0.3	0.07
S. sp 01 (D.Catchpole 1356)	SRp	0.5	0.07
S. sp 02 (D.Catchpole 0862)	Cae	4.4	0.55
S. sp 03 (D.Catchpole 1530)	Cae	0.2	0.01
S. sp 05 (D.Catchpole 1303)	Cae	0.2	0.01
S. sp 07 (D.Catchpole 0858)	Cae	0.2	0.01
S. sp 08 (D.Catchpole 1215)	SRp	0.9	0.14
S. sp 21 (D.Catchpole 0788)	Cae	0.6	0.07
S. sp 24 (D.Catchpole 979)	Cae	0.2	0.01
S. sp 25 (D.Catchpole 1172)	Cae	0.2	0.01
S. sp 26 (D.Catchpole 0516)	Cae	0.6	0.04
Trichopilia sp 01 (D.Catchpole 1357)	Asc	0.2	0.01
Trichosalpinx chamaelepanthes (Rchb.f.) Luer (D.Catchpole 1189)	Lep	0.6	0.08
T. notosibirica (Hashimoto) Luer (D.Catchpole 1399)	Lep	0.2	0.01
T. scabridula (Rolf) Luer (D.Catchpole 1337)	Lep	3.0	0.82
T. sp 01 (D.Catchpole 1186)	Lep	0.2	0.01
T. sp 02 (D.Catchpole 1138)	Lep	0.6	0.07
Xylobium sp 01 (D.Catchpole 1463)	Asc	0.2	0.01
cf. Orchidaceae sp 02 (D.Catchpole 1159)	Asc	0.2	0.01
cf. Orchidaceae sp 03 (D.Catchpole 1194)	Cae	3.3	0.30
cf. Orchidaceae sp 04 (D.Catchpole 1247)	Asc	0.2	0.01
cf. Orchidaceae sp 05 (D.Catchpole 1334)	Cae	0.3	0.12
cf. Orchidaceae sp 06 (D.Catchpole 1392)	Asc	0.2	0.03
cf. Orchidaceae sp 07 (D.Catchpole 1393)	Asc	0.2	0.01
cf. Orchidaceae sp 08 (D.Catchpole 0982)	Asc	0.3	0.02
Oxalidaceae			
Oxalis sp 01 (D.Catchpole 1518)	LRp	0.5	0.03
Piperaceae			
Peperomia sp 01 (D.Catchpole 0949)	Asc	11.7	1.15
P. sp 02 (D.Catchpole 0945)	Asc	0.3	0.02
Piper sp 01 (D.Catchpole 0944)	Asc	0.3	0.02
cf. Piperaceae sp 01 (D.Catchpole 1065)	LRp	0.5	0.03
cf. Piperaceae sp 02 (D.Catchpole 1380)	Asc	0.3	0.02
cf. Piperaceae sp 03 (D.Catchpole 0917)	Asc	0.2	0.01

Appendix I (cont)

List of taxa found on the surveyed tree. Lifeform abbrev. and frequency values are defined in the text. All vouchers / specimens in cultivation are housed at OXA.	Lifeform	Cl. Freq. (%)	Rel. Freq. (%)
Polypodiaceae			
Campyloneurum amphostenon (Klotzsch) Fee (D.Catchpole 1381)	Pnd	0.6	0.06
C. sp 01 (D.Catchpole 1522)	SCr	0.2	0.01
Niphidium crassifolium (L.) Lell (D.Catchpole 1125)	LCr	1.7	0.16
Pecluma sp 02 (D.Catchpole 0572)	SCr	0.2	0.01
Polypodium sp 01 (D.Catchpole 0029)	LCr	0.2	0.01
P. sp 02 (D.Catchpole 0029)	LCr	0.6	0.12
cf. Polypodiaceae sp 01 (D.Catchpole 0402)	LCr	0.6	0.04
cf. Polypodiaceae sp 02 (D.Catchpole 0948)	SCr	0.8	0.07
Rubiacea			
Cosmibuena sp 01 (D.Catchpole 1044)	Asc	3.6	0.28
Vittariaceae			
Antrophyum lineatum (Sw.) Kaulf. (D.Catchpole 0943)	Pnd	0.3	0.03
Vittaria lineata (L.) Sm. (D.Catchpole 1378)	Pnd	0.2	0.04
Undetermined Taxa			
cf. Dicotyledonae sp 01 (D.Catchpole 0520)	Asc	0.9	0.08
cf. Dicotyledonae sp 02 (D.Catchpole 0891)	Asc	0.2	0.01
cf. Dicotyledonae sp 03 (D.Catchpole 1002)	Clb	0.5	0.04
cf. Dicotyledonae sp 04 (D.Catchpole 1176)	Asc	0.2	0.02
cf. Dicotyledonae sp 05 (D.Catchpole 1267)	Asc	0.3	0.02
cf. Pteridophyta sp 01 (D.Catchpole 0278)	Pnd	0.2	0.01